ASPECTS OF THE BEHAVIOUR OF THE RED-BELLIED PADEMELON *Thylogale billardierii* (DESMAREST 1822) IN CAPTIVITY

by

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Male *Thylogale billardierii*

Female *Thylogale billardierii*

SUMMARY

Aspects of the behaviour of a captive group of red-bellied pademelons (*Thylogale billardierii*), were investigated, concentrating on three main areas, *viz.* diel activity-patterns, sexual interactions and agonistic interactions. Some data pertaining to mother-offspring relationships were also collected.

T. billardierii exhibited a marked peak in feeding at around sunset, with other conspicuous peaks occurring late at night and in the early morning. Conversely, peaks of resting behaviour occurred mainly at midday and, in general, two distinct peaks were evident during the night. Locomotory activities were most frequent during the period immediately preceding dawn.

Grooming behaviour was performed at relatively constant diel levels; however, there was evidence of this activity occurring at greater frequencies before and after rest periods.

Although patterns of the various diel activities were generally similar in all of the subjects studied, there were some disparities in the times of performance of certain behaviours between individual subjects, possibly related to the social structure of the group. The results are discussed in relation to what is known of the activity-patterns of free-ranging *T. billardierii* and those of other macropod species.

As well as indications of temporal variations in behaviour patterns, there was evidence of spatial-temporal stratification of certain behaviours, notably resting activities.

Quantitative data were collected on sexual interactions. Males were the active participants in these, both in terms of initiating such interactions and performing specific and distinctive behaviours within bouts of sexual interactions. Analyses of behavioural events occurring in the context of anoestrous courting yielded consistent trends with

respect to the temporal ordering of activities. Male *T. billardierii* did not distribute their attentions equally among potentially available females but evidenced definite preferences for certain individuals.

Observed instances of copulation are described and compared with previous descriptive accounts of the behaviour in this species and in other species of macropods. There was some evidence that access to oestrous females was determined aprioristically, by the dominance-status of males.

The agonistic behaviour of *T. billardierii* was also investigated. Generally, linear hierarchies existed within each monosexual group. However, when all subjects were considered together a non-linear organization was noted to occur. Position in the individual hierarchies was related to weight but, at least in the case of female subjects, this was shown not to be the only factor involved. A relatively low level of aggression occurred between female subjects and also in male-female interactions. Given the relative stability of the social positions of individuals and low observed frequencies of dominance-reversals, it is suggested that individual recognition (possibly based on olfactory cues gained by nose-sniffing behaviour) plays a prominent role in the maintenance of consistent social relationships in captive *T. billardierii*.

Ritualized fighting behaviour of male *T. billardierii* is described, and its possible function is discussed. Grass-pulling and other visual displays which occur in the context of male-male interactions are described and their relationship with similar displays occurring in other macropods is considered.

In mother-offspring interactions it was found that the young was primarily responsible for the maintenance of proximity, but that the mother played a greater role in maintaining proximity at larger distances.

Evidence is presented of the possibility of individual recognition of the distress vocalization of young *T. billardierii* by their mothers.

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CHAPTER 1

INTRODUCTION

Members of the family Macropidadae occupy virtually every type of terrestrial habitat in Australia (Kaufmann 1974a,b) but behavioural studies on this group have been limited, particularly in comparison with the wealth of information available about their eutherian analogues, the ungulates.

The cryptic habits and nocturnal tendencies of most species of macropodid marsupials are not conducive to investigations of their behaviour, especially in natural conditions. Consequently, such studies have been concentrated on the larger members of the family, the kangaroos, euros and large wallabies while smaller species of macropod have been virtually ignored. Furthermore, studies thus far attempted have generally been almost entirely qualitative and few investigators have concentrated on quantifying aspects of the behaviour of macropods.

The red kangaroo *Macropus rufus (=Megaleia rufa)*, has undoubtedly been the subject of the greatest amount of attention with respect to behaviour studies. Descriptions of the behaviour of this species have been presented, based on both captive groups (Sharman and Calaby 1964; Russell 1970b) and on free-ranging populations (Frith and Calaby 1969; Croft 1981a). Quantitative studies on certain aspects of agonistic, drinking, sleeping and mother-offspring behaviours have also been undertaken (Russell 1970a; Russell and Nicholls 1972; Cicala *et al.* 1970; Russell 1973; Croft 1981a). The arid habitat which this animal occupies has prompted studies on the relationship between ambient temperatures and behaviour (Russell 1971; Russell and Harrop 1976). Aspects of various daily activities have been studied in free-ranging *M. rufus* (Caughley 1964b; Croft 1981a).

Several features of the behaviour of the euro *M. robustus erubescens*, have been described by Ealey (1967), Russell (1969) and

Croft (1981b), the latter author having undertaken a detailed study on social behaviour of this species. Quantitative studies on drinking behaviour have been presented by Ealey (*op. cit.*) and Russell and Nicholls (*op. cit.*).

Social behaviour in the eastern grey kangaroo *M. giganteus,* has been studied in the field by Caughley (1964b), Kirkpatrick (1966), Grant (1973, 1974), Kaufmann (1975) and in captivity by Grant (1973, 1974) and Coulson (1977)*. Herrmann (1967 after Russell and Giles 1974) investigated pouch-cleaning behaviour in this species, while its general maintenance activities have been described by Grant (1974). The western grey kangaroo *M. fuliginosus,* has been the object of only a single behavioural study, involving a captive population (Coulson *op. cit.*)*.

Activity-patterns have been investigated in *M. fuliginosus* (Stewart and Setchell 1974), in *M. giganteus* (Caughley 1964b; Grant 1974) and on a comparative basis, in both species (Coulson 1978).

A single, brief study on free-ranging antilopine wallaroos *M. antilopinus,* has been undertaken to date, on the social behaviour of this species (Croft 1982). Captive subjects of the same species have also been the subject of a study in a zoological garden (Coulson 1980)*. Russell and Richardson (1971) found that this species was typically non-solitary.

An extensive study of the behaviour of free-ranging whiptail wallabies *M. parryi* has been reported by Kaufmann (1974a).

Agonistic interactions in the Bennetts wallaby, *M. rufogriseus frutica,* have been described, based on captive groups (LaFollette 1971; Murböck 1975) and Mooney and Johnson (1979) reported on the home-range and movements of this subspecies. Kaufmann (1974a,b) performed cursory observations on the red-necked wallaby, *M. rufogriseus banksianus*

and Coulson (1978) studied patterns of daily activity in the latter subspecies. Murböck (1976, 1977 after Ganslosser 1980) investigated various aspects of social behaviour in the species in a zoo study.

Behavioural studies on other members of the genus *Macropus* have been sparse. Russell and Giles (1974) made a detailed study of pouch-cleaning in the Tammar wallaby *M. eugenii* and the incidences of allogrooming between females of this species has also been the subject of comments (Giles and Russell 1975). Maynes (1973) described reproductive behaviour in the parma wallaby, *M. parma*.

Home-ranges and movements have been described in the swamp wallaby *Wallabia bicolor* (Edwards and Ealey 1975), the single extant species of the genus *Wallabia*.

The quokka *Setonix brachyurus*, is probably the most extensively investigated representative of the smaller macropodines. Packer (1969) studied various aspects of the behaviour of this species in an enclosure. Field populations of the species have been investigated, with respect to their ecology and in this context certain features of behaviour have been described by Dunnett (1962), Holsworth (1967), Packer (1965), Kitchener (1970 after Kaufmann 1974a, 1972) and Nicholls (1971).

Members of the genus *Thylogale*, one species of which genus is the object of this study, have been investigated only on a relatively few occasions. Ganslosser (1978) briefly described fighting behaviour in *T. brunii*. Johnson (1977a), in the course of a study of the ecology of the red-necked pademelon *T. thetis*, reported certain solitary and social behaviour-patterns in this species. Morton and Burton (1973) observed a captive group of red-bellied pademelons *T. billardierii*, in a zoological garden and described various features of their behaviour. Johnson (1978) reported on a study on home-ranges of male *T. billardierii* and on the diel use of pastures by this species. McCartney (1978) noted certain aspects of the reproductive behaviour of this

species.

Some aspects of the social behaviour of rock-wallabies of the genus *Petrogale* have been described in three species *P. inornata* (Dwyer 1972)*, *P. puella* (Davies 1979)* and the brush-tailed rock-wallaby, *P. penicillata* (Joblin 1981)*.

Tree-kangaroos (*Dendrolagus*) have similarly been neglected, especially with respect to field-studies. Ganslosser (1977) observed different captive groups of *D. dorianus* and *D. inustus* maintained in several zoological gardens and described their behaviour.

There has been a conspicuous paucity of behavioural studies on members of the subfamily Potoroinae. Stodart (1966) described the behaviour of the burrowing bettong, *Betongia lesueur,* based on subjects observed in an enclosure. Johnson (1978) and Mooney and Johnson (1979) reported on the home-ranges and movements of the Tasmanian bettong, *B. gaimardi*. Various aspects of the maintenance activities of the long-nosed potoroo, *Potorous tridactylus* have been investigated (Buchmann in preparation) and also agonistic interactions in the species have been described (Buchmann 1977, after Ganslosser 1980). Johnson (1980b) observed a captive group of rufous bettongs,*Aepyprymnus rufescens* and selected features of their behaviour.

Investigations of curiosity and exploratory behaviour in macropods have been limited to studies on *M. rufus* and *M. eugenii* (Glickman and Scroges 1966 after Russell and Pearse 1971; Russell and Pearse *op. cit.*). Newman (1961 after Kirkby 1977) tested the learning ability of an adult female *M. rufus* on visual discrimination tasks and Munn (1964 after Kirkby *op. cit.*) under more stringent conditions, studied the ability of three kangaroos (species not stated) to learn to discriminate between vertically and horizontally oriented stimuli.

Composite reports on several species of macropods, including descriptions of various features of their behaviour have been presented by Brown (1974) on species dewelling in arid zones and Russell (1974b)

on large macropods. Russell (1974a) reviewed current ecological studies on marsupials and reported on behavioural studies on a range of macropods.

Ganslosser (1980) presented an annotated bibliography of social behaviour in the family Macropodidae.

In view of the paucity of behavioural studies on macropods, the current project was undertaken to investigate aspects of behaviour of the *Thylogale billardierii* in an enclosure and in particular, to attempt to quantify various types of activity exhibited by this species. Three main areas were selected for attention: the diel activity-patterns of behaviour, sexual interactions and agonistic interactions of the subjects. In addition, in the course of this study it was intended to gain more qualitative information about the behaviour of this species.

Because of the changing state of the taxonomy of macropods in recent years, specific names used in this introduction and throughout the remainder of this thesis are based on Kirsch and Calaby (1977) in an effort to avoid ambiguity and the common names of species are those recommended by the Australian Mammal Society (Strahan 1980).

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* Full details of study not presented.

CHAPTER 2

GENERAL ASPECTS OF THE PRESENT STUDY AND OF THE BIOLOGY OF *Thylogale billardierii*

2.1 THE MAINTENANCE OF CAPTIVE SUBJECTS

Captive specimens of *Thylogale billardierii* were maintained in two enclosures at the University of Tasmania. All observational and experimental studies were pursued in a 18.1 m x 24.3 m (439.8 m^2) compound which was situated on sloping ground of *ca.* 20^{o} in gradient. Numerous species of plants were present within the enclosure, with the dominant dicotyledon being hawthorn bushes, *Crataegus monogyna*. Subjects grazed and browsed on almost all vegetation present.

Subjects were provided with a constant supply of commercial lucerne- and rat-pellets placed in a food hopper and water was also supplied. Bread, apples, cabbage-leaves and a variety of other food items were provided *ad libitum*; however, the distribution of these food items was never performed less than 2h before an observation session.

A total of eleven subjects were used during the course of the study (three males, five females, one juvenile female and two juvenile males) and subjects not studied at any particular stage of the investigations were maintained in a 1 ha enclosure situated behind and above the compound used for observation. Further details pertaining to individual subjects are presented in Appendix 1.

All specimens observed in this study were already held in captivity at the commencement of the present investigation and had been obtained previously from the wild, from captive populations at Monash University, Victoria, or from breeding stock at the University of Tasmania.

Observations were made from a small green canvas hide (1 m x 1 m x 1.8 m) and later from a larger observation room (1.5 m x 1.5 m x 1.8 m) constructed of galvanized iron, both of which were positioned within the enclosure (Figure 2.1). The enclosure was divided into quadrats and a peripheral region was delineated by the positioning of wooden stakes *ca.* 1.5 m high. Reflective tape was placed near the top of each stake in order to facilitate discrimination of them at night.

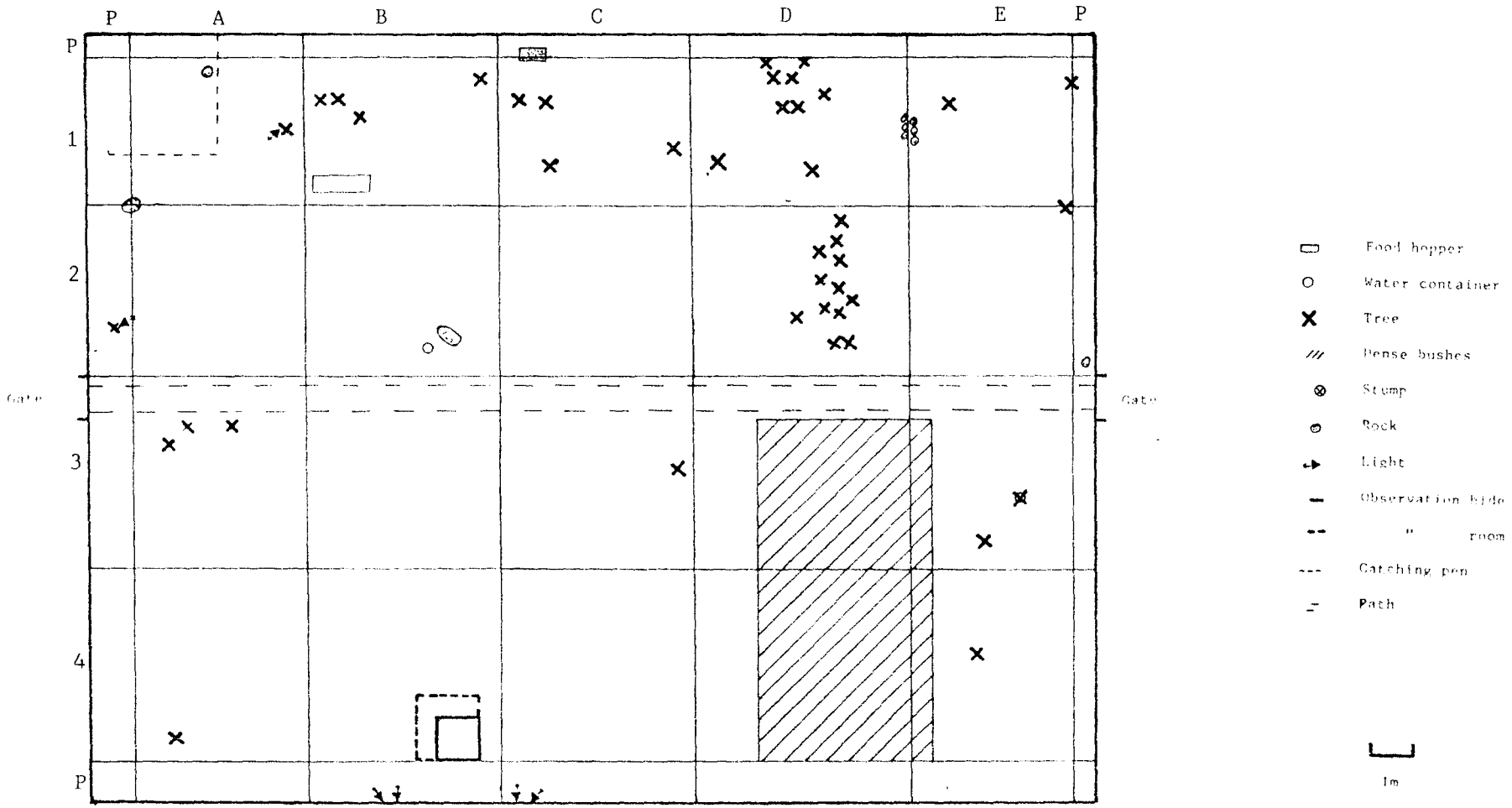


FIGURE 2.1: Plan of lower enclosure. Quadrats indicated by lettering and numbers. (P= peripheral).

All subjects were individually recognizable because of the presence of various characteristics such as notches in the ears, fitted leather collars or differences in size.

2.2 GENERAL BIOLOGY OF *Thylogale billardierii*

2.2.1 General Description

Thylogale billardierii is one of four extant species of the genus *Thylogale*, commonly termed pademelons.

The pelage of *T. billardierii* is typically dark brown to dark grey-brown on the upper regions of the body and buff with a rufous tinge on the lower regions, especially the lower abdomen (Johnson and Rose in press). For this reason it is often commonly termed the red-bellied pademelon. A faint strip of lighter fur is often evident on the upper femural region.

There is an apparent sexual dimorphism in regards to weight in this species. Males may reach weights of up to 12 kg, the mean weight being 7.0 kg whereas the average weight of adult females is 3.9 kg. The mean head and body length is 630 mm in males and 560 mm in females and the mean length of the tail is 417 mm in males and 320 mm in females (Johnson and Rose *op. cit.*).

T. billardierii is similar in size to other species of *Thylogale* (Johnson 1977a) and is intermediate in size to other species of macropod also found in Tasmania; *Macropus rufogriseus frutica* and *Bettongia gaimardi* (Johnson and Rose *op. cit.*).

2.2.2 Taxonomy

The generic name *Thylogale* was first used by Gray in 1837 (Tate 1948 after Johnson 1977a). The presence of a labial notch at or towards the rear of 1^3 (posterior upper incissors) is the main diagnostic feature of the genus (Hope 1981). The type species of this genus is *T. thetis*

(Johnson 1977a). The four extant species included in this genus are the red-necked pademelon, *T. thetis* (Lesson 1828), the red-legged pademelon, *T. stigmatica* (Gould 1860), *T. brunii* (Schreber 1778) and *T. billardierii* (Desmarest 1822). A further species, *T. christenseni*, has been described, from archaeological sites in Irian Jaya, Indonesia, but the present status in Indonesia and New Guinea is not known (Hope *op. cit.*).

The generic name is derived from the classical Greek words *thylakos*, meaning sack or pouch and *gale* meaning weasel. The second half of the generic name is probably a derivative reference to the marsupial nature of these animals, by analogy with *Phascogale* (Strahan 1981).

T. billardierii was named after J.J.H. LaBillardière (botanist in D'Entrecasteaux voyage of the Recherche and Esperence in search of the missing Lapérouse), who obtained the original specimen (Strahan *op. cit.*, Troughton 1965).

T. billardierii is somewhat aberrant from the other species of *Thylogale* in that the labial notch of the 1^3 does not extend as far posteriorly in this species, as in others (Hope *op. cit.*). Ride (1957) placed *T. billardierii* in a different genus (*Protomendon*) on the basis of this difference, however he later (Ride 1970) replaced it within the genus *Thylogale* (Johnson 1977a). Cytologically, the species is closely allied to other species of this genus than to the larger wallabies (Sharman 1961).

2.2.3 Distribution and Ecology

The genus *Thylogale* extends from the Bismarck Archipelago, 3^{o}S, 150^{o}E, through New Guinea and the east coast of continental Australia to the southern coast of Tasmania, 43^{o}S 147^{o}E (Johnson 1977a). *T. billardierii* is widely distributed throughout Tasmania and occurs on many of the larger Bass Strait islands (Green 1974; Hope 1974). The species formerly occurred in southern Victoria and south-eastern South Australia but is now apparently extinct in these areas (Green *op. cit.*; Johnson

and Rose *op. cit.*).

The present distribution of the genus *Thylogale* is shown in Figure 2.2. *T. stigmatica* is sympatric in parts of its range with both *T. thetis* and *T. brunii*. Calaby (1966) found that both *T. thetis* and *T. stigmatica* occurred in rainforests, including lantana edges of some areas, in large patches of lantana or areas formerly covered by rainforest and in the dense shrubby ground-layer of wet gullies. However, the two species did not occur together but occupied exclusively small patches of rainforest or discrete parts of larger patches. In New Guinea, *T. stigmatica* is usually associated with underbrush of gallery-rainforests but is also found in savannah-woodland and, occasionally, in grasslands of the south-central New Guinea lowlands, whereas *T. brunii* inhabits man-made and alpine grasslands and areas of secondary growth (Ziegler 1977).

T. billardierii is found in the dense vegetation of wet sclerophyll forests, rainforests and tea-tree scrubs, as well as in open, grassy, dry sclerophyll forests where dense vegetation suitable for cover is found. In all these habitats it forms well defined and regularly-used runways (Johnson and Rose *op. cit.*).

The diet of *T. billardierii* consists of short green grasses and herbs, as well as browse from taller woody plants (Johnson and Rose *op. cit.*). Individuals of this species may move up to 2 km to feeding areas from their daytime resting places (Tighe *et al.* 1981). Johnson (1978) reported that male *T. billardierii* have overlapping home-ranges of an average size of 156 ha. Individuals observed in the same study moved out onto pasture to feed at night, but localised their activities to close to the forest edge.

Johnson (1980) stated that in *T. thetis* the mean size of home-ranges was 13.86 ha and that this species also restricted its nocturnal feeding activities to areas of pasture adjacent to forest. The large differences in the sizes of home-ranges of *T. billardierii* and *T. thetis* are probably

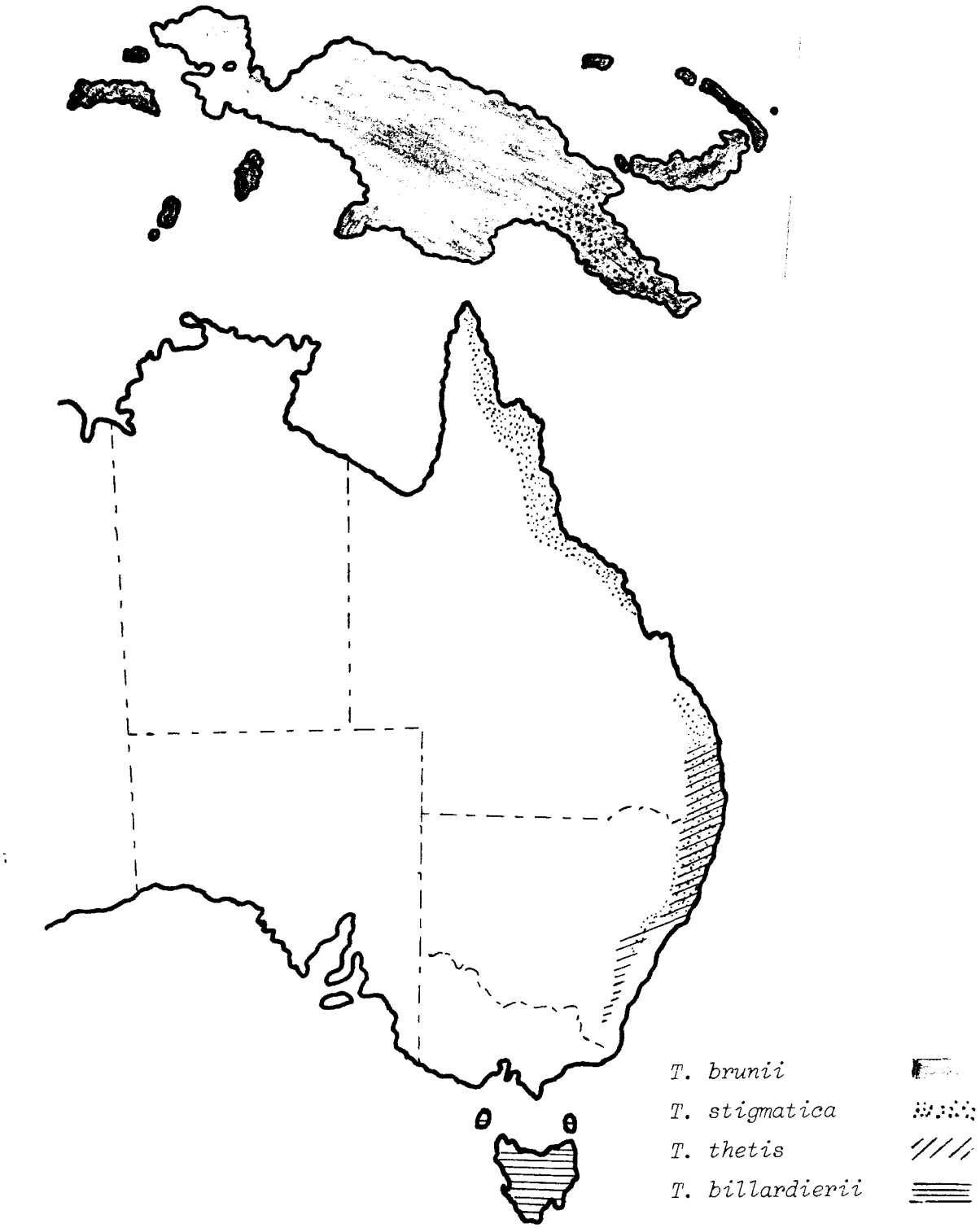


Figure 2.2. Distribution of the genus *Thylogale* (after Johnson 1977a).

related to the different habitats (open dry sclerophyll forest *c.f.* dense rainforest) in which these studies were pursued rather than any species specific differences.

2.2.4 Reproduction, Growth and Population Biology

Reproduction in *T. billardierii* conforms to the basic macropodid pattern. The mean length of gestation is 30.2 days which is similar to the mean duration of the oestrous cycle (30.3 days). Post-partum mating occurs in this species and the resulting embryo is maintained as a dormant blastocyst (Rose and McCartney 1982a).

T. billardierii exhibits seasonal peaks in breeding, most births occurring in the months April, May and June (Rose and McCartney 1982a). The average duration of pouch-life is 202 days and vacation of the pouch coincides precisely with paturition. Infants first begin to make excursions out of the pouch at *ca.* 180 days and are completely covered by fur by 144-160 days (Rose and McCartney 1982b).

Sexual maturity is attained after *ca.* 14 months in both males and females (Rose and McCartney 1982a).

The life-expectancy of *T. billardierii* in the wild is *ca.* 4.25 years (McCartney 1978). *T. billardierii* is abundant throughout Tasmania and is commercially exploited for its meat and pelt. Large numbers of pademelons may be taken by hunters in any one season but the level fluctuates greatly from year to year (Guiler 1957; Johnson 1977b). This species may reach pest proportions in some areas and poisoning-schemes have, in some cases, been implemented to control numbers (Mollison 1960a; Tighe *et al., op.cit.*).

T. billardierii have been reported to live in colonies (Troughton 1965). Rose and Johnson (*op. cit.*) stated that feeding aggregation of ten or more individuals may form but there is no evidence of colonial social structure or of other persistent social bonds between individuals. *T. billardierii* are reputed to have a docile disposition but occasionally

squabbles may occur (Green 1973). However, severe fighting may develop between captive males (Rose *pers. comm.*).

2.3 QUALITATIVE INVENTORY OF THE BEHAVIOUR OF *Thylogale billardierii*

2.3.1 Postures Assumed by Stationary Subjects

The terminology adopted in the present study is largely based on Russell (1970b).

(a) Standing Erect (Plate 2.3.1)

In this posture, the animals stood with their backs at *ca.* 45° - 90° angle to the ground and the crown of the head was elevated above the level of the dorsum, the arms were usually closely adposed to the chest. The tail was generally extended posteriorly and rested on the ground. Before and after assuming a seated posture, animals often stood erect with their tails between the hind legs and directed forward.

(b) Standing Crouched (Plate 2.3.2)

The animals stood with their backs at an angle of 45° or less to the ground and the crown of the head was in a position below the highest part of the torso. This posture differed from a comparable posture observed in the red kangaroo, *Macropus rufus* (Russell 1970b) in that pademelons typically held their arms close to the chest, whereas in kangaroos the forelimbs rested on the ground, barely in contact with it.

(c) Standing in Quadrupedal and Tripedal Stances (Plate 2.3.3)

A distinction was made between these stances and the standing-crouched posture, because of the fact that in pademelons the forelimb(s) appeared to support a more substantial proportion of the body weight than in *M. rufus* in which species the forepaws rest only lightly on the

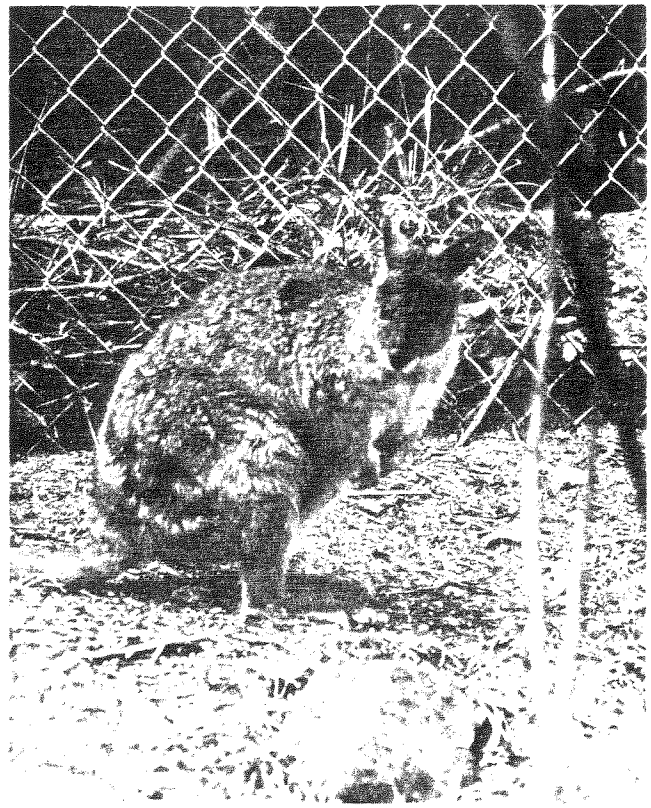


PLATE 2.3.1: Standing erect

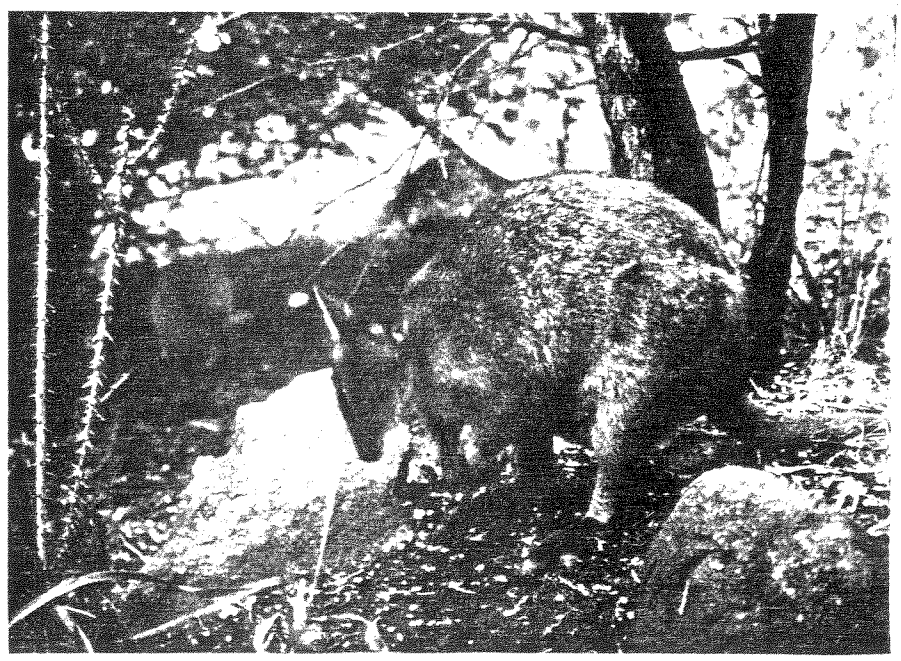


PLATE 2.3.2: Standing crouched

PLATE 2.3.3(a): Standing quadrupedal

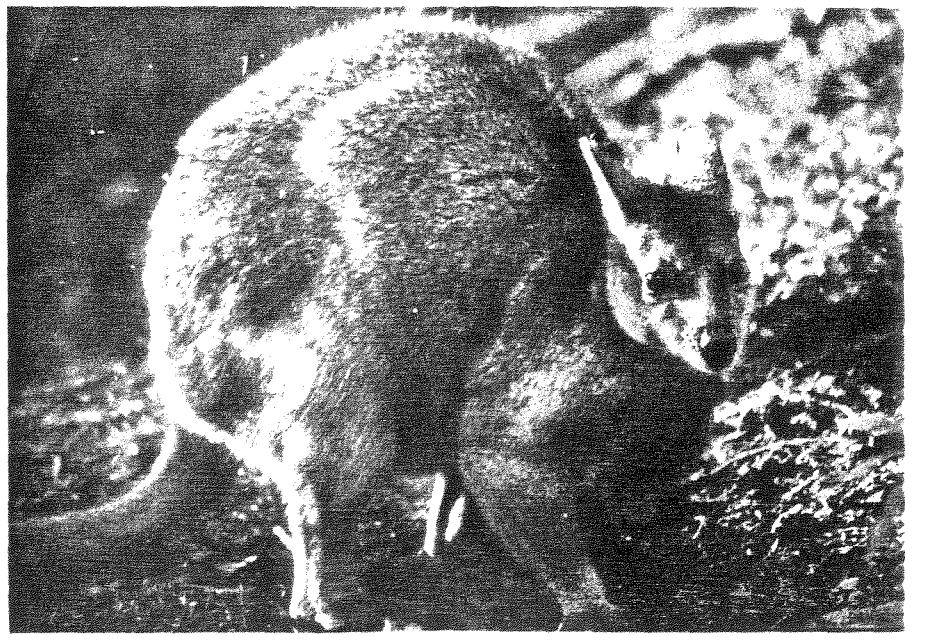


PLATE 2.3.3(b): Standing tripedal

PLATE 2.3.4(a): Seated-down,head raised

PLATE 2.3.4(b): Seated-down,head tucked under

ground (Russell 1970b).

(d) Seated-Down (Plate 2.3.4)

This was the normal resting posture of *T. billardierii*. The legs and tail of the animals were extended anteriorly and the rump rested on the ground; typically the arms were folded under the body or were extended forward and rested on, or near, the tail. Similar sitting postures have been described in *T. thetis* (Johnson 1977a) and *M. parryi* (Kaufmann 1974a); however, in the latter species the abdomen does not rest on the legs. *M. rufus* assume a similar posture in order to groom certain regions of the body such as the tail, pouch and the hind limbs (Russell 1970b).

In *T. billardierii* the head was either raised (Plate 2.3.4a) or held close under the chest (Plate 2.3.4b) while the animal was in the seated position. Pademelons usually held their heads under the thorax only during bouts of nocturnal resting and they also appeared to sleep in this position. M1 was the only subject observed to sleep during the day.

(e) Seated-Upright

This posture was only observed in females that carried large pouch young. It was similar to the seated-down posture, except that in this stance the trunk of the individual was held vertically, often in contact with a tree or the fence. It differed from a standing position in that the weight of the animal was mainly supported on its rump, rather than on the feet; nevertheless, it was sometimes difficult to discern whether or not an animal was standing erect or seated upright when it was at some distance from the observer.

(f) Lying-Down

Individuals were occasionally observed to adopt a lying-down posture similar to that described in *M. rufus* (Russell 1970b). The animals lay on their sides, with the head usually held clear of the ground and oriented

at *ca.* 90° from the trunk. Morton and Burton (1973) stated that *T. billardierii* was observed lying-down only while exposed to the sun in winter. This was generally the case in this study; however, on two relatively warm days (temperature *ca.* 30°C), some individuals were noted to have adopted this posture while resting in the shade.

2.3.2 Locomotion

Two distinct gaits have been identified in *T. billardierii*, slow progression and bipedal hopping (Windsor and Dagg 1971).

(a) Slow Progression

This gait was employed by pademelons when moving over relatively small distances and while travelling slowly, for example when grazing. The tail did not appear to provide any substantial support during the time when the hind feet were not in contact with the ground.

(b) Bipedal Hopping

In this gait, the forelimbs were held folded against the chest and the body inclined forward. At higher velocities, the head and body were maintained almost horizontal to the ground and the upward displacement achieved by each hop was very slight. The tibia to femur ratio is *ca.* 1 and closer in value to *Potorous tridactylus* than to other Tasmanian macropods (Rose *pers. comm.*). These features are apparently a reflection on the preferred habitat of this species *viz.* areas with dense undergrowth through which they construct runways (Johnson and Rose in press), which would probably be conducive to the development of flat and agile method of locomotion.

2.3.3 Feeding and Drinking

Animals grazed on the grasses present in the enclosure and all accessible branches of trees were browsed. In attempts to reach the

higher branches of trees, animals stood high on the extremities of the digits of the hind feet and tried to grasp the ends of branches with their mouth and forepaws in order to pull them downwards. It is possible that the tail assisted in maintaining balance during this process.

The forepaws were used to remove and to hold pellets from the food hopper, and to manipulate slices of bread, pieces of apple etc., while eating.

Merycism, or regurgitation (Barker *et al.* 1963) was occasionally observed in captive *T. billardierii*. It is estimated that during this study it occurred about once in every two or three days per subject. This process has been described in many species of the family Macropodidae in captive populations (Moir *et al.* 1956; Barker *et al.* 1963; Russell 1970b; Schürer 1972 after Ganslosser 1977; Morton and Burton 1973; Ganslosser 1977; Johnson 1980b) and in free-ranging *T. billardierii*, *M. rufogriseus frutica* (Mollison 1960b), *M. parryi* (Kaufmann 1974a), *Petrogale puella* (Davies 1979) and *M. rufus* (Croft 1981a).

In the present study as in that of Morton and Burton (*op. cit.*), food material was often spilled from the mouth during the process of regurgitation and such material was usually reingested by the animals. On a single occasion (20.6.1982), F5 regurgitated, M3 supplanted F5 and then ate the bolus that F5 had expelled. In another instance, M1 and F1 both fed on food-material that F1 had regurgitated.

Merycism may aid digestion in the macropodines by stimulating salivary secretions (Hume 1982).

During drinking, water was apparently lapped up by the tongue.

2.3.4 Comfort Movements

(a) Autogrooming

Pademelons were able to reach almost every part of the bodies in

the course of grooming activities. The forepaws were employed to scratch the head, flanks, back, abdominal area, hind legs and tail. Pademelons also wiped the sides of their muzzles with their forepaws after licking them.

The hind feet were used to scratch the head, neck and shoulder regions. When they were employed for this purpose, the large claw of the fourth digit was curled inward, presumably to prevent damage to it or the area being scratched and the syndactylus claws of the 2nd and 3rd digits were mainly used in grooming.

Pademelons used their mouths to lick and nibble the fur on the fore- and hindlimbs, the abdomen,flanks, genitalia, and tail. Particular attention was given to the manus and pes.

While licking the genitalia, males often held the testicles with their forepaws, apparently to facilitate cleaning. Females held the pouch open with the forepaws and inserted their snouts when grooming it.

Licking of the forelimbs was commonly performed on very hot days or after animals had been engaging in large amounts of vigorous activity such as running around (for example, when they were chased for the purpose of capturing and examining them). Such grooming has been reported in similar contexts in *M. rufus* (Russell 1970b, 1971; Russell and Harop 1976, Croft 1981a). The possible contribution of licking to thermoregulation has not yet been established (Russell 1971). Prevention of licking in *Setonix brachyurus* had no effect on body temperatures (Bentley 1960 after Russell 1971). The inner margin of the forelimbs in kangaroos are well supplied with superficial blood vessels (Dawson 1977).

(b) Shaking the Body

This was occasionally observed in subjects, usually during rain. It was also seen when animals were harassed by insects (flies) and on two occasions when yellow-throated honeyeaters, *Lichenostomus flavicollis*,

were removing fur from pademelons, presumably using it to line their nests (Sharland 1981).

(c) Stretching

Pademelons were sometimes observed to stretch their bodies, usually after rest-periods. This behaviour involved standing fully erect and either drawing the shoulders up and back or thrusting the arms out in front of the body as far as they could be extended. The animals were also occasionally observed to stretch their hind limbs out and forward while in the seated-down posture; during this process the legs were elevated from the ground.

2.3.5 Vocal Communication

Three types of vocalizations were identified and are discussed in more detail in Chapter 7.

(a) Hiss-growl

This sound was made by both males and females during intraspecific encounters and when they were handled by the investigator. Morton and Burton (1973) stated that this sound is produced by dominant individuals in agonistic interactions. Although it was often difficult to locate the sources of sounds precisely, in almost all cases when this was positively identified it was the fleeing animal, rather than the aggressor which made the vocalization. The exception to this was noted when the alpha male, M1, was heard to utter both the clucking (see below) and this vocalization while interacting with another male M2, during the period a female was in oestrous (Section 4.4.2). It is possible in this case that the vocalization was slightly different to the normal hiss-growl, electronic analysis of each vocalization would need to be performed to verify this.

(b) Clucking

This vocalization was heard in three different circumstances. Males were heard to utter it while engaging in sexual following of a female (Section 4.2.2) or when supplanting another individual (Section 5.3.2).

Females also emitted this sound when they were observed signalling to their young (Section 6.5.2).

(c) Hiss

This was emitted by pouch-young when they were removed or had fallen out from the pouch (Section 6.5.2).

2.3.6 Other Forms of Communication

(a) Alarm Foot Thump

When suddenly disturbed, *T. billardierii* typically thumped their hind feet down hard during their first few hops when fleeing. This action apparently caused nearby individuals to become alert but generally did not induce them to flee. This behaviour has been described in *T. thetis* (Johnson 1977a), *Aepyprymnus rufescens* (Johnson 1980b), *M. parryi* (Kaufmann 1974a), *M. giganteus* (Croft 1982), *M. fuliginous* (Croft 1982), *M. robustus erubescens* (Croft 1981b) and *M. rufus* (Croft 1981a).

(b) Olfactory

This aspect of behavioural communication is generally difficult to investigate, but may often be a very important factor. Numerous indirectly disclosed expressions of behaviour probably related to olfactory communication were observed in *T. billardierii*. No investigation of the presence and functional roles of secretory glands have been undertaken

to date on this species and in the absence of such information definite conclusions on the involvement of olfactory communication cannot be made; however, where such factors are believed to be of potential importance, they are mentioned in the course of the ensuing discussion.

(c) Visual

Johnson (1977a) suggested that sexual dimorphism, with respect to the larger chest and more robust musculature of the arms of male *T. thetis* has some signal function, indicating to other males the relative social ranking of individuals. This feature probably also has some importance in conveying signals between male *T. billardierii*; furthermore, size-differences are presumably important in communication during male-female and female-female interactions.

In the context of male-male interactions, two other types of behavioural events were observed and are believed by the author to have some potential signal-value *viz.* grass-pulling and standing full-stretch (Section 5.3.2). These are discussed in Section 5.4.4.

In some instances the absence of an overt reaction (change in on-going behaviour) by an individual to some action performed by another individual may itself communicate information to the latter, e.g. failure of a female to retreat when grasped around the flanks by a male may indicate to the male receptivity of the female. Such "non-reactions" may therefore be regarded as visual signals; however, in the majority of cases the existence of this type of passive transference of information must remain a matter for speculation.

(d) Tactile

Individual *T. billardierii* engage in substantial amounts of touching, pushing, striking, holding, biting and licking in a variety of amicable, agonistic and sexual contexts. These events may have some

communicatory function and are further discussed in the relevant sections of the text.

2.3.7 Types of Interactions Between Individuals

(a) Nose-sniffing (Plate 2.3.5)

When approaching another individual pademelons commonly oriented their noses to a position immediately below the muzzle of the other individual. The latter often reciprocated this action. After performing such behaviour, the animals engaged in amicable, agonistic or sexual activities towards other individuals; however, the types of subsequent reactions were generally consistent for each individual e.g. after nose-sniffing at F4, M3 invariably attempted to make sexual advances toward it; after nose-sniffing at F3, F5 always retreated rapidly and subsequent to nose-sniffing F1, M1 either attempted to court it, allogroom it, induce it to "rest together" (see below) or apparently ignored it. It is therefore, tentatively hypothesised that *T. billardierii* can recognize their conspecifics, if not individually, at least as members of some class of the population (male or female, old or young etc.) by means of this activity.

Morton and Burton (1973) suggested that nose-sniffing behaviour constituted a form of threat; however, from the results of this study no evidence supporting this contention was obtained.

This behaviour-pattern is common in macropodids during non-agonistic encounters (Croft 1982).

(b) Resting Together (Plate 2.3.6)

Male and female *T. billardierii* were occasionally observed to adopt a resting position in contact with each other. The posture of each animal was similar to the seated-down posture, except that the male placed its head over the nape of the female's neck and typically rested

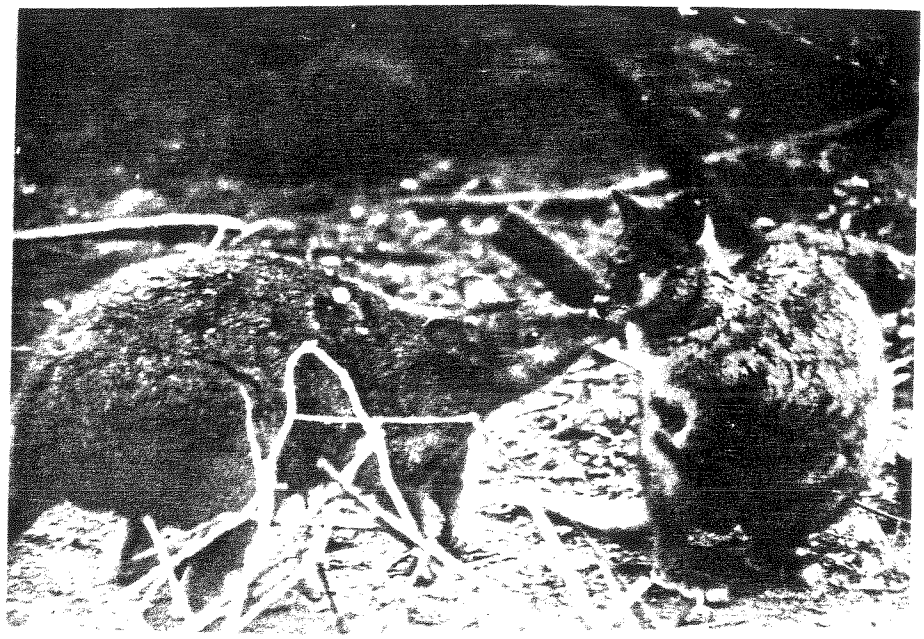


PLATE 2.3.5: Nose-sniffing

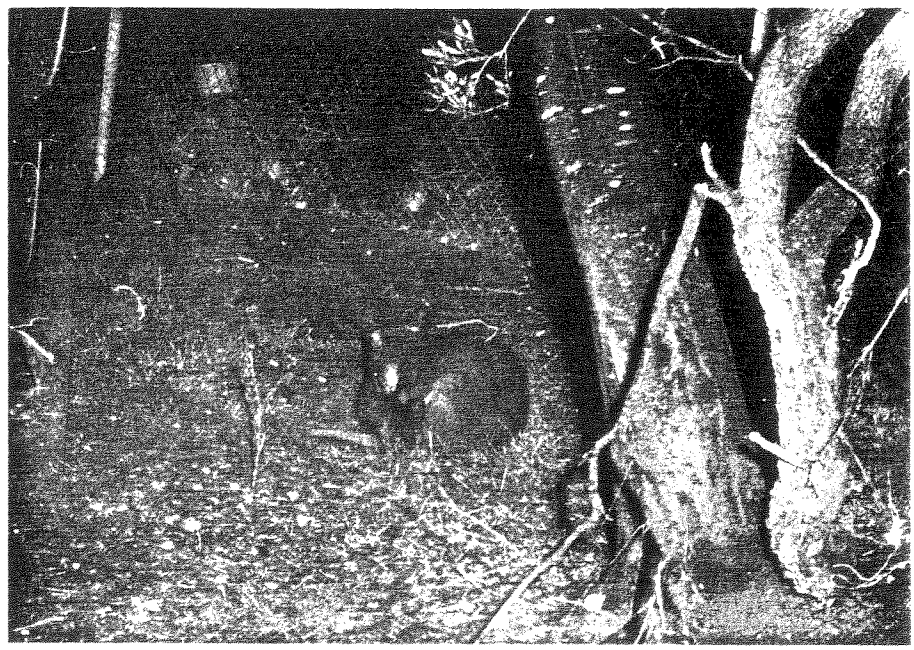


PLATE 2.3.6: Resting together

its forelimbs on the neck and upper back region of the latter, the longitudinal axes of the animals were, therefore, at approximately right angles during this activity. In almost every observed instance, it was the male that initiated this behaviour and occasionally it actively prevented the female from leaving. Males and females were usually observed to assume this position at night. It is possible that this was an artifact of captivity; however, it was observed to be performed by both adult males, M1 and M2.

The resting-together position was also observed to be assumed by a mother and its young-at-foot. Although these animals occasionally rested together during the day, it was of a much more frequent occurrence at night (in terms of relative proportions of time spent resting together and resting apart). On some occasions M1, F1 and F6 (F1's offspring) were all observed to rest together.

This type of behaviour between males and females has not been described in any other species of the subfamily Macropodinae but in some members of the subfamily Potoroinae individuals share communal rest-sites, at least in captivity (Stodart 1966; Schürer 1978a after Ganslosser 1980). Schürer (1978 after Ganslosser 1980) reported that *M. fuliginosus* and *M. agilis* rest in contact but due to lack of access to the original report the author is uncertain of the exact form taken by such resting behaviour.

If this behaviour is typical of *T. billardierii*, it may be expected to be highly adaptive in view of the low ambient temperatures to which these animals are often exposed. It may be relevant to note that individual rested-together generally only at night, when their preferred resting-positions were in the open section of the enclosure and the temperatures were much lower (often near 0°C) while during the day the animals rested in the thicketed region of the enclosure (Section 3.3.2).

(c) Allogrooming

Grooming (in all cases by licking) of conspecifics was observed in several contexts *viz.* sexual interactions, agonistic interactions between male subjects, mother-offspring interactions and when males and females were resting together. In most cases, grooming was directed at the head and neck regions of the recipients but was also sometimes directed at the back and in the grooming of offspring by their mother, most regions of the body were groomed, particularly during the stages when the young were not yet permanently out of the pouch. Allogrooming has been noted as a frequent activity in male-female interactions in *P. puella* (Davies 1979), *M. antilopinus* (Croft 1982) and has also been reported in *B. lesueuri* (Stodart 1966), *S. brachyurus* (Kitchener 1970 after Kaufmann 1974a), *M. eugenii* (Croft 1982), *M. rufogriseus frutica* (LaFollette 1971), and *M. giganteus* (Croft 1982). Male-male allogrooming is common in *M. antilopinus* and *M. fuliginosus* (Croft 1982) and has been observed in *M. parryi* (Kaufmann 1974a), *M. giganetus* (Croft 1982), and *M. rufus* (Croft 1981a). Female-female allogrooming has been observed in *M. eugenii* (Giles and Russell 1975), *M. rufogriseus frutica* (LaFollette 1971), *M. fuliginosus* and *M. antilopinus* (Croft 1982). Adult female *T. billardierii* were never observed to groom one another in the course of this study.

Mutual grooming in the context of mother-offspring interactions is widespread in the family Macropodidae and is further discussed in Chapter 6.

(d) Sexual Interactions and Agonistic Interactions

These are treated in detail elsewhere (Chapters 4 and 5).

2.3.8 Miscellaneous Behaviours

(a) Fence-running (Plate 2.3.7)

Captive subjects were observed to ambulate regularly along sections of the perimeter of the enclosure. Individuals typically moved along the fence-line, by hopping or slow progression, for a few metres, occasionally pausing and often apparently sniffing at the fence, then continuing on in their original direction or, more frequently, in the opposite direction. The nett result of this activity was a continuous process of patrolling a section of the perimeter, usually concentrated at the corners. This behaviour was common after dusk but the great majority of the activities occurred immediately before dawn. Different subjects engaged in fence-running to varying extents (Section 3.4.3).

(b) Chewing

While resting during the day-time animals were often observed to perform chewing movements with their mouths. In most cases, no food had been ingested for some time previously (up to *ca.* 2 h in some instances) and no evidence of regurgitation was observed before the onset of this activity.

In ruminants, nitrogen derived from circulating blood urea and other endogenous sources of nitrogen are continually returned to the rumen with the saliva (Brown and Main 1967). Recycling of nitrogen has been demonstrated in *S. brachyurus* and *M. robustus erubescens* (Brown 1964 after Brown and Main 1967).

It is possible that *T. billardierii* ingest saliva in order to recycle some metabolic products; however, at this stage little is known of this aspect of the biology of the species.

Dellow (1979 after Hume 1982) suggested that similar chewing observed in other macropods was pursued to stimulate secretion of saliva and this may aid digestion by increasing the pH of the stomach.

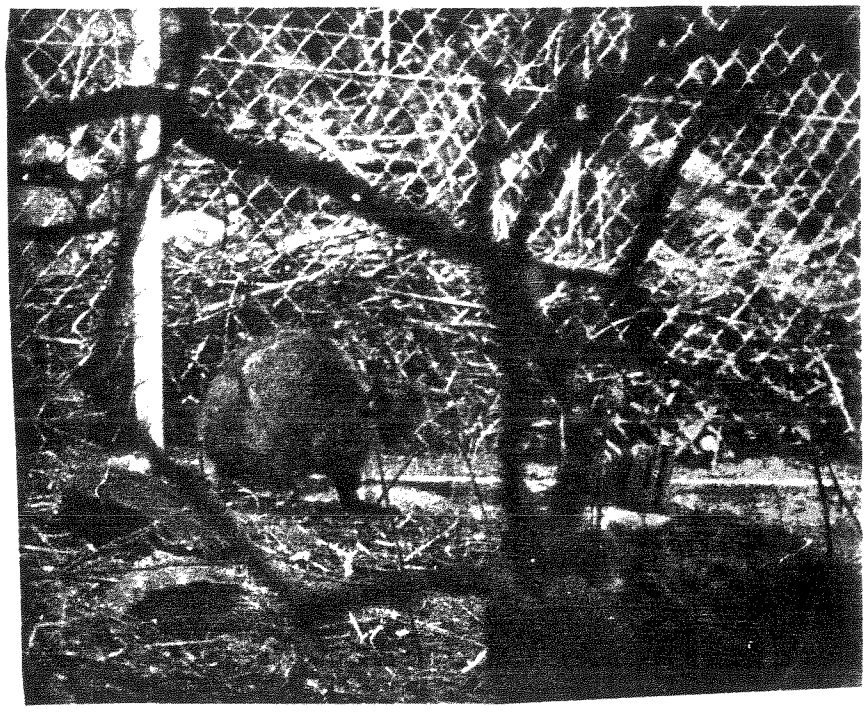


PLATE 2.3.7: Fence-running

CHAPTER 3

DIEL ACTIVITY-PATTERNS

3.1 INTRODUCTION

It is generally recognized that many species of animals tend to exhibit consistent trends in the diel distribution of their behaviour-patterns. However, there is a conspicuous paucity of quantitative studies on this aspect of ethology. Leuthold (1977) attributed this deficiency, at least in the case of free-ranging ungulates, to the obvious difficulties in obtaining sufficient data, given the methods currently available. These restrictions are also true of studies on macropodid marsupials.

In investigations of animals using enclosures, many of these problems can be overcome, for example viewing the animals at night may be feasible. However, activity-patterns exhibited in even the most naturalistic conditions by captive animals are not necessarily strictly comparable to those exhibited by free-living conspecifics. Excessively broad generalizations from studies undertaken on captive subjects is unwise, but by taking into account their limitations, they may yield useful information, especially when they are combined with field studies.

The majority of species of macropods are generally described as being either nocturnal or crepuscular (Coulson 1978). Various aspects of the diel activity of *Megaleia rufa* have been studied in the field by Caughley (1964b) and subsequent observations on captive animals did not disclose any major differences of activity periods (Russell 1970b). Studies on activity-patterns recorded over 24 hour periods have been undertaken on *Macropus giganteus* (Caughley *op cit.*; Grant 1974; Coulson *op. cit.*), on *M. fuliginosus* (Stewart and Setchell 1974; Coulson *op. cit.*) and on *M. rufogriseus banksianus* (Coulson *op. cit.*). Field studies have also been made on the diel activities of *Setonix brachyurus* by Packer (1965) and Nicholls (1971) and also on captive individuals of the same species (Packer 1969). Stodart (1966) examined aspects of

the diel behaviour of *Bettongia lesueuri* in an enclosure.

All of these studies employed only one or two behavioural categories as criteria of "activity". Other, more quantitative studies of changes in activity-patterns have concentrated on seasonal changes based on diurnal observations, especially on arid-zone animals.

Thylogale billardierii is reputed to be crepuscular (Troughton 1965) or nocturnal (Hyett and Shaw 1980; Johnson and Rose, in press). However, no quantitative studies of its diel activity have hitherto been published. The National Parks and Wildlife Service of Tasmania, having undertaken census studies of wallabies and possums, incidentally collected data on the diel use of pastures by *T. billardierii* and radio-tracking data were obtained for four males of this species showing their diel movements (Johnson 1978).

The present study was attempted to determine the temporal and spatial distribution of behaviour in *T. billardierii* maintained in an enclosure, and to investigate the occurrence of any differences between individuals of different sexes, reproductive states and ages.

3.2 METHODS

The subjects were observed in a series of two hour sessions for a total of ninety-six hours, yielding data for four complete 24 hour periods. Recorded observation samples were distributed over a ten-week period, extending from 17 May 1982 to 28 August 1982. The animals were viewed from a 1 m x 1 m x 1.8 m canvas hide positioned inside the enclosure (Figure 2.1).

During the initial stages of this investigation the author assumed his position in the hide ca. 30 minutes before the commencement of each observation period but this was subsequently reduced as it was found that the animals generally resumed their ongoing behaviour (whether this was passive or active) very shortly after the observer entered the

hide.

Observations on the animals were assisted by the use of 12 x 50 binoculars and a 100 Watt spotlight. Illumination of the compound was achieved by means of 4 x 150 Watt red lights and two white lights covered with red filters of 80 and 100 Watts respectively (Figure 2.1).

The method of sampling employed was the "instantaneous" sampling technique described by Altamann (1974). This was selected for several reasons, *viz.* not all parts of the enclosure were visible from the observation point, hence individuals moved in and out of the author's field of vision, rendering focal animal sampling impracticable; the method permitted all visible animals to be observed in turn, consequently data on the degree of synchrony of behavioural states between animals were obtained.

In practice, the enclosure was scanned (in a clockwise direction in all samples in an attempt to eliminate unintentional bias) and the current behaviour pursued by each animal at the time when it was first seen, as well as its position in the enclosure, were recorded on a standard protocol-sheet. After the initial scanning, if all animals were not sighted a second scan was performed using binoculars (during daylight periods) or spotlight (at night). Prior to the commencement of these observation periods, brief tests were undertaken, shining light from the spotlight on individuals that were in full view. It was noted that this did not appear to alter the ongoing behaviour of the subjects, even when they were only a short distance (*ca.* 2 m) from the hide.

Samples were taken at 5 minute intervals. Each sample required a period of up to a minute to complete and the animals were not observed for at least 20 seconds (usually 30 seconds) before every sample was taken, also in an attempt to avoid bias. Intervening times were used to score agonistic and sexual interactions (Sections 4.2.1 and 5.2.1).

The restrictions imposed by this method of sampling are that rare behaviour categories and those of very brief duration tend to be missed (Slater 1978). As a consequence of the method of recording employed, transitional movements could be scored as belonging to either the preceding or ensuing behavioural state. For example, if an animal raised its leg to scratch or lowered it after scratching, this could be recorded as either grooming or standing. In the majority of instances the ensuing event was recorded.

Categories of behaviour were selected so that they were as discrete and exclusive as possible, consisting of homogenous acts and to be descriptive (criteria implying causal or functional interpretations were excluded from consideration) as is recommended by Slater (*op. cit.*). The categories used are shown in Table 3.1 and are described qualitatively in Section 2.3. For purposes of recording, categories were represented by simple coded symbols (e.g. GM→P = licking or biting of the pes) and the position of the subject was recorded in relation to grid-references (Figure 2.1). General conditions pertaining to weather, such as the occurrence of rain, were also recorded.

During this phase of the investigation, seven *T. billardierii* were maintained in the enclosure (M1, M3, F1, F3, F4, F5 and F6, see Appendix 1); F6, the offspring of F1, was leaving the pouch for brief periods at the commencement of the sampling period and vacated the pouch permanently during the course of this phase of the study.

TABLE 3.2.1 Behavioural categories used in recording the diel activity of subjects.

Standing	Full Stretch
	Erect
	Crouched
	Quadrupedal
	Tripedal
Seated Down	
Seated Up	
Lying Down	
Locomotion	Slow progression
	Bipedal
Feeding	
Drinking	
Grooming	With Mouth
	With Forepaws
	With Hindpaws
	Pouch
Regurgitation	
Nose Sniffing	
Genital Sniffing	
Pouch Investigation	
Coquet	
Cuffing	
Grappling	
Grasping	
Grasspulling	
Suckling	

3.3 RESULTS

3.3.1 Temporal Distribution of Behavioural Elements

For analysis of the temporal distribution of selected behavioural elements, analysis of variance was employed in all cases, as this permits interactions between variables (e.g. subjects, sampling periods, times of the day, etc.) to be identified. Sampling-sessions were grouped into four 24 hour periods (referred to as "days" in all subsequent discussion). The distribution of the sampling-sessions over each day is shown in Table 3.3.1, together with mean times of sunrise and sunset.

TABLE 3.3.1 Distribution of the dates of sampling-sessions for each 24 hour aggregate and the corresponding mean times of sunrise and sunset.

Day	Mean	Range	Sunrise	Sunset
1	25.5.1982	May 17th to May 28th	0726h	1649h
2	11.6.1982	May 28th to June 30th	0740h	1642h
3	30.6.1982	June 7th to July 21st	0744h	1646h
4	14.7.1982	June 27th to July 28th	0749h	1655h

The results of the analyses of all categories of behaviour are presented in Tables 3.3.2 to 3.3.15. Three elements, "lying down", "seated up" and "seated down" were combined in a single category, "resting". "Seated up" was only recorded in F1 and consisted of only 5.9% of her total resting time; "lying down" was recorded in M1, F1 and F6 and constituted 5.0%, 6.4% and 3.6% respectively of their total resting time. "Standing full-stretch" was not included in the "standing" category for the purpose of analysis but in the "other" behavioural category, as it was considered to reflect a completely unrelated motivational state (associated with either feeding or fighting behaviour, Section 2.3).

TABLE 3.3.2 Two-way analysis of variance of the frequencies of feeding recorded over the four sample days (using the six subjects as replicates).

Source	d.f.	Variance (M.S.S.)	F-ratio	P
Sample-days	3	5.13	1.19	n.s.
Hours of day	23	58.42	13.56	<0.001
Interaction	69	12.24	2.84	<0.001
Residual	480	4.31		
TOTAL	575	7.43		

TABLE 3.3.3 Three-way analysis of variance of the frequencies of feeding recorded for the six subjects grouped into males, females advanced pouch-young and females with very early stage or no pouch-young (using sample-days as replicates).

Source	d.f.	Variance (M.S.S.)	F-ratio	P
1. Between groups of subjects	2	6.05	1.23	n.s.
2. Within groups of subjects	1	0.25	0.05	n.s.
3. Hours of day	23	57.23	11.61	<0.001
1 x 2 Interaction	2	15.90	3.22	<0.05
1 x 3 Interaction	46	7.36	1.49	<0.05
2 x 3 Interaction	23	6.20	1.26	n.s.
1 x 2 x 3 Interaction	46	5.54	1.12	n.s.
Residual	432	4.93		
TOTAL	575	7.35		

TABLE 3.3.4 Two-way analysis of variance of the frequencies of resting recorded over the four sample days (using the six subjects as replicates).

Source	d.f.	Variance (M.S.S.)	F-ratio	P
Sample-days	3	10.1	1.04	n.s.
Hours of day	23	172.96	17.89	<0.001
Interaction	69	31.42	3.25	<0.001
Residual	480	9.67		
TOTAL	575	18.81		

TABLE 3.3.5 Three-way analysis of variance of the frequencies of resting recorded for the six subjects (grouped as in Table 3.3.3, sample-days used as replicates).

Source	d.f.	Variance (M.S.S.)	F-ratio	P
1. Between groups of subjects	2	11.57	0.96	n.s.
2. Within groups of subjects	1	56.88	4.70	<0.05
3. Hour of the day	23	160.99	13.30	<0.001
1 x 2 Interaction	2	165.02	13.63	<0.001
1 x 3 Interaction	46	14.26	1.18	n.s.
2 x 3 Interaction	23	10.27	0.84	n.s.
1 x 2 x 2 Interaction	46	12.26	1.01	n.s.
Residual	432	12.10		
TOTAL	575	35.29		

TABLE 3.3.6 Two-way analysis of variance of the frequencies of standing recorded over four sample-days (using the six subjects as replicates).

Source	d.f.	Variance (M.S.S.)	F-ratio	P
Sample-days	3	5.64	1.64	n.s.
Hours of day	23	44.56	12.92	0.001
Interaction	69	7.02	2.04	0.001
Residual	480	3.45		
TOTAL	575	5.53		

TABLE 3.3.7 Two-way analysis of variance of the frequencies of standing recorded for the six subjects observed (using sample-days as replicates).

Source	d.f.	Variance (M.S.S.)	F-ratio	P
Individual subjects	5	26.71	7.50	<0.001
Hours of day	23	44.21	12.42	<0.001
Interaction	115	4.16	1.17	n.s.
Residual	432	3.56		
TOTAL	575	5.50		

Contrasts between individual subjects (d.f. = 1,432)

Pairs of s.s.	F-ratio	P
M1, F1	4.12	<0.05
M1, F3	18.71	<0.001
M1, F4	25.92	<0.001
M1, F5	2.12	n.s.
M1, M3	1.89	n.s.
F1, F3	5.27	<0.001
F1, F4	9.38	<0.001
F1, F5	0.33	n.s.
F2, M3	0.42	n.s.
F3, F4	0.59	n.s.
F3, F5	8.24	<0.001
F3, M3	8.69	<0.001
F4, F5	13.22	<0.001
F4, M3	13.79	<0.001
F5, M3	0.01	n.s.

TABLE 3.3.8 Two-way analysis of variance of the frequencies of locomotion recorded for the six subjects observed.

Source	d.f.	Variance (M.S.S.)	F-ratio	P
Individual subjects	5	15.63	3.81	<0.01
Hours of day	23	19.39	4.73	<0.001
Residual	115	4.10		
TOTAL	143	6.96		

Contrasts between individual subjects (d.f. = 1,115)

Pairs of s.s.	F-ratio	P
M1, F1	0.13	n.s.
M1, F3	3.98	<0.05
M1, F4	6.23	<0.05
M1, F5	7.73	<0.01
M1, M3	6.23	<0.05
F1, F3	5.53	<0.05
F1, F4	8.13	<0.01
F1, F5	9.84	<0.01
F1, M3	8.13	<0.01
F3, F4	0.25	n.s.
F3, F5	0.62	n.s.
F3, M3	0.25	n.s.
F4, F5	0.08	n.s.
F4, M3	0.00	n.s.
F5, M3	0.08	n.s.

TABLE 3.3.9 Two-way analysis of variance of times when individual subjects (n = 6) were not visible.

Source	d.f.	Variance (M.S.S.)	F-ratio	P
Individual subjects	5	75.28	3.37	<0.01
Hours of day	23	34.26	1.53	n.s.
Residual	115	22.33		
TOTAL	143	26.10		

Contrasts between individual subjects (d.f. = 1,115)

Pairs of s.s.	F-ratio	P
M1, F1	1.42	n.s.
M1, F3	1.81	n.s.
M1, F4	10.88	<0.01
M1, F5	5.39	<0.05
M1, M3	10.68	<0.01
F1, F3	0.02	n.s.
F1, F4	4.44	<0.05
F1, F5	1.28	n.s.
F1, M3	4.31	<0.05
F3, F4	3.82	n.s.
F3, F5	0.96	n.s.
F3, M3	3.70	n.s.
F4, F5	0.96	n.s.
F4, M3	0.00	n.s.
F5, M3	0.90	n.s.

TABLE 3.3.10 Two-way analysis of variance of the frequencies of auto-grooming for the six sample subjects.

(a) Pouch grooming included in female's scores of grooming (subjects grouped as in Table 3.3.3; hours of day used as replicates).

Source	d.f.	Variance (M.S.S.)	F-ratio	P
Between groups of subjects	2	14.38	2.60	n.s.
With groups of subjects	1	45.56	8.24	<0.01
Interaction	2	0.27	0.05	n.s.
Residual	138	5.53		
TOTAL	143	5.86		

(b) Pouch grooming excluded from female's scores of grooming (subjects grouped as in Table 3.3.3; (hours of day used as replicates).

Source	d.f.	Variance (M.S.S.)	F-ratio	P
Between groups of subjects	2	3.44	0.72	n.s.
Within groups of subjects	1	4.34	0.91	n.s.
Interaction	2	12.19	2.55	n.s.
Residual	138	4.79		
TOTAL	143	4.87		

(c) Pouch grooming excluded from female's scores of grooming (subjects ungrouped).

Source	d.f.	Variance (M.S.S.)	F-ratio	P
Individual subjects	5	8.26	1.74	n.s.
Hours of day	23	6.01	1.27	n.s.
Residual	115	4.76		
TOTAL	143	7.08		

TABLE 3.3.11 Three-way analysis of variance of pouch grooming in female subjects (n = 4). Females were grouped into individuals with advanced pouch young (F1, F5) and individuals with early stage or no pouch young (F3, F4).

Source	d.f.	Variance (M.S.S.)	F-ratio	P
1. Between groups of subjects	1	8.17	5.14	<0.05
2. Within groups of subjects	1	2.04	20.63	<0.001
3. Hours of day	5	2.39	6.04	<0.001
1 x 2 Interaction	1	1.50	3.79	n.s.
1 x 3 Interaction	5	2.17	5.47	<0.001
2 x 3 Interaction	5	0.94	2.38	<0.05
1 x 2 x 3 Interaction	5	2.38	3.16	<0.05
Residual	72	0.40		
TOTAL	95			

TABLE 3.3.12 Two-way analysis of variance of frequencies of allogrooming recorded for the six subjects observed.

Source	d.f.	Variance (M.S.S.)	F-ratio	P
Individual subjects	5	10.41	14.52	<0.01
Hours of day	23	0.565	0.79	n.s.
Residual	115	0.717		
TOTAL	143	1.031		

Contrasts between individual subjects (d.f. = 1,115)

Pairs of s.s.	F-ratio	P
M1, F1	72.63	<0.001
M1, F3	176.76	<0.001
M1, F4	176.76	<0.001
M1, F5	176.76	<0.001
M1, M3	176.76	<0.001
F1, F3	22.77	<0.001
F1, F4	22.77	<0.001
F1, F5	22.77	<0.001
F1, M3	22.77	<0.001
F3, F4	0.00	n.s.
F3, F5	0.00	n.s.
F3, M3	0.00	n.s.
F4, F5	0.00	n.s.
F4, M3	0.00	n.s.
F5, M3	0.00	n.s.

TABLE 3.3.13 Two-way analysis of variance of the frequencies of drinking recorded for the six sample subjects.

Source	d.f.	Variance (M.S.S.)	F-ratio	P
Individual subjects	5	0.78	1.52	n.s.
Hours of day	23	1.06	2.05	<0.01
Residual	115	0.52		
TOTAL	143	0.61		

TABLE 3.3.14 Two-way analysis of variance of the frequencies of sexual interactions recorded for male subjects (n = 2)

Source	d.f.	Variance (M.S.S.)	F-ratio	P
Individual subjects	1	0.08	0.77	n.s.
Hours of day	23	1.58	1.46	n.s.
Residual	23	1.08		
TOTAL	47	1.30		

TABLE 3.3.15 Two-way analysis of variance of the frequencies of non-sexual interactions recorded for the six sample subjects.

Source	d.f.	Variance (M.S.S.)	F-ratio	P
Individual subjects	5	1.51	2.19	n.s.
Hours of day	23	1.27	1.85	<0.05
Residual	115	0.69		
TOTAL	143	0.81		

For comparison of the distribution of feeding, resting and grooming behaviours, subjects were divided into three subgroups *viz.* males, females with advanced pouch young (F1, F5) and females with very early-stage or no pouch young (F3, F4). As there were no significant differences between days, total scores obtained for four day periods, for each individual subject, were treated in the analysis of locomotion, autogrooming, allogrooming, drinking, sexual interactions, non-sexual interactions and when subjects were not visible.

Based on previous observations some *a priori* considerations were employed in grouping certain behavioural categories into sexual interactions and other interactions. Thus, "pouch investigation", "genital investigation", "coquet" and "flank-grasping" were included in the former when performed by a male in relation to a female subject. Grasping, cuffing, nose-sniffing and grappling were included in the latter category. Male subjects only, were scored as sexually interacting, females being essentially passive during such encounters.

The diel distributions of various categories of behaviour are presented in Figures 3.3.1 to 3.3.12. A general diel activity-cycle for *T. billardierri* observed in captivity, based on the percentage time individual subjects were engaged in each behavioural category per hour (summed for the six subjects), is presented in Figure 3.3.13.

As F6 (the offspring of F1) was permanently out of the pouch for a part of the study period, she was omitted from the analyses (except where indicated).

3.3.2 Spatial Distribution of Behavioural Elements

The sectors of the enclosure utilized by subjects for resting are shown in Table 3.3.16. Marked preferences for particular sectors were exhibited by all individuals; however, their preferred positions for diurnal resting differed from those utilized during nights. Although positions were recorded only in terms of the presence of the subjects

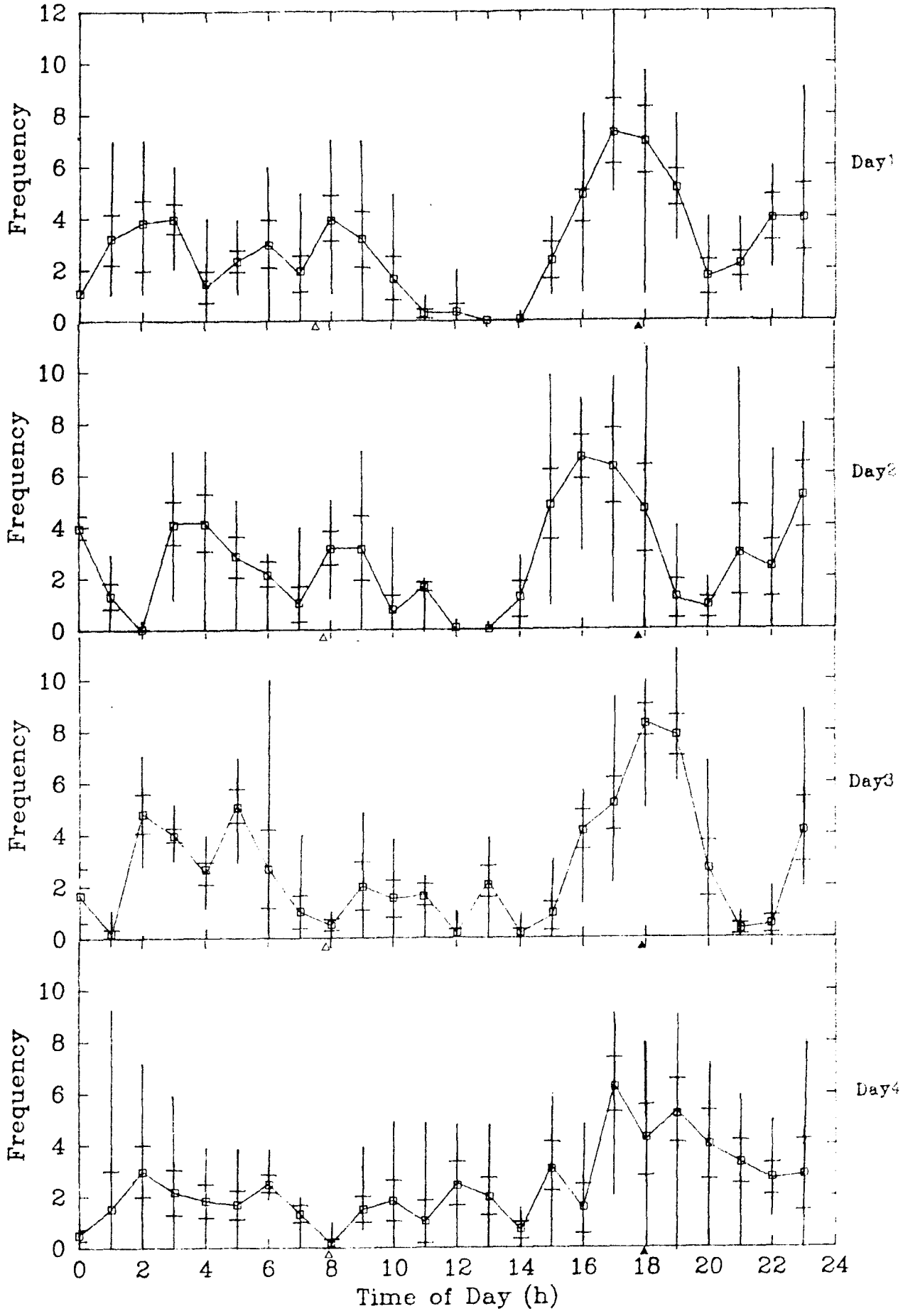


FIGURE 3.3.1: Mean, standard error and range of feeding scores of subjects (n=6) for each "day". (n.b. The maximun score for any subject during any one hour sample is 12.)

△ mean time of sunrise

▲ mean time of sunset

FIGURE 3.3.2: Mean, standard error and range of resting scores of subjects (n=6) for each "day".

△ mean time of sunrise

▲ mean time of sunset

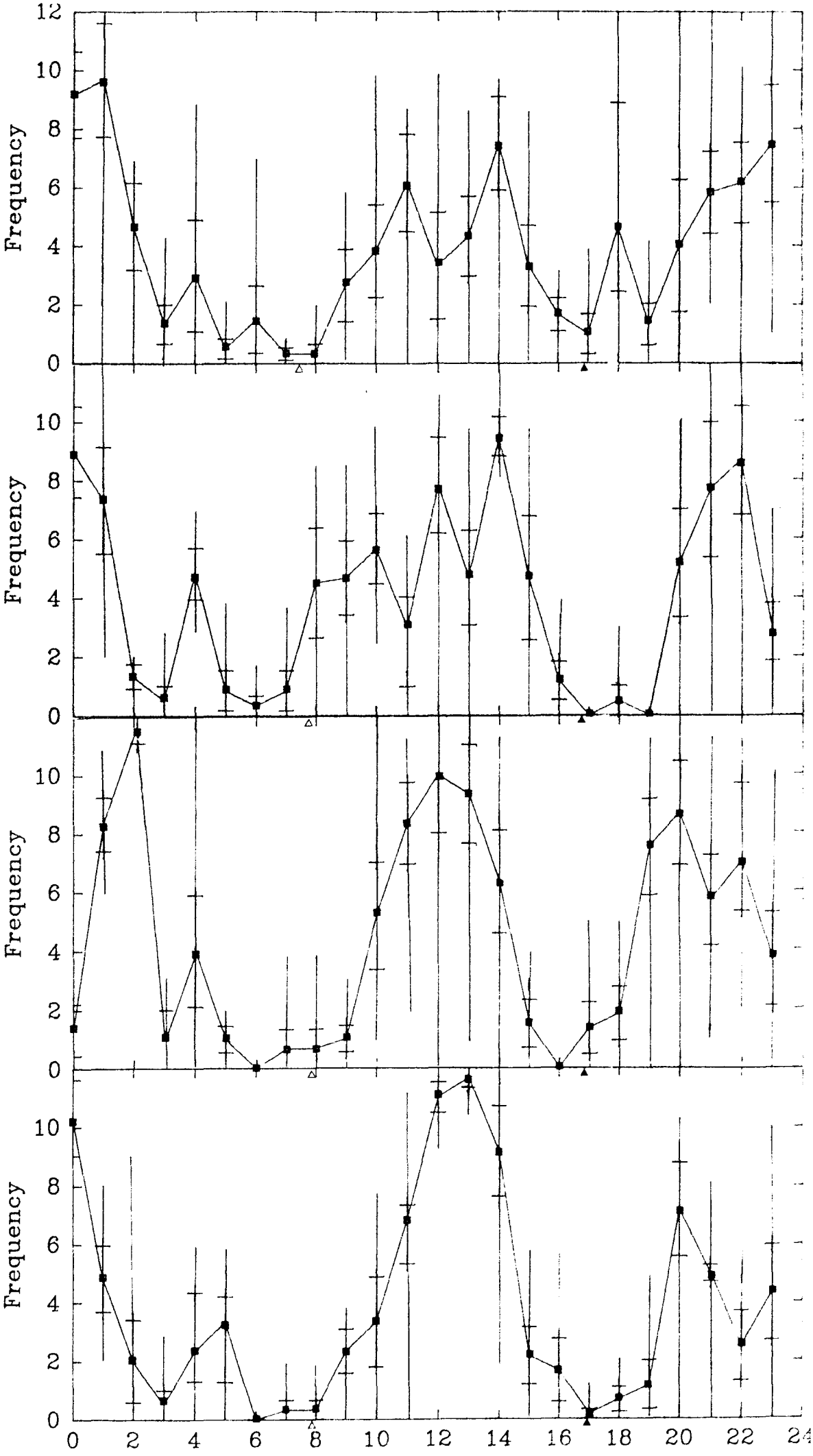
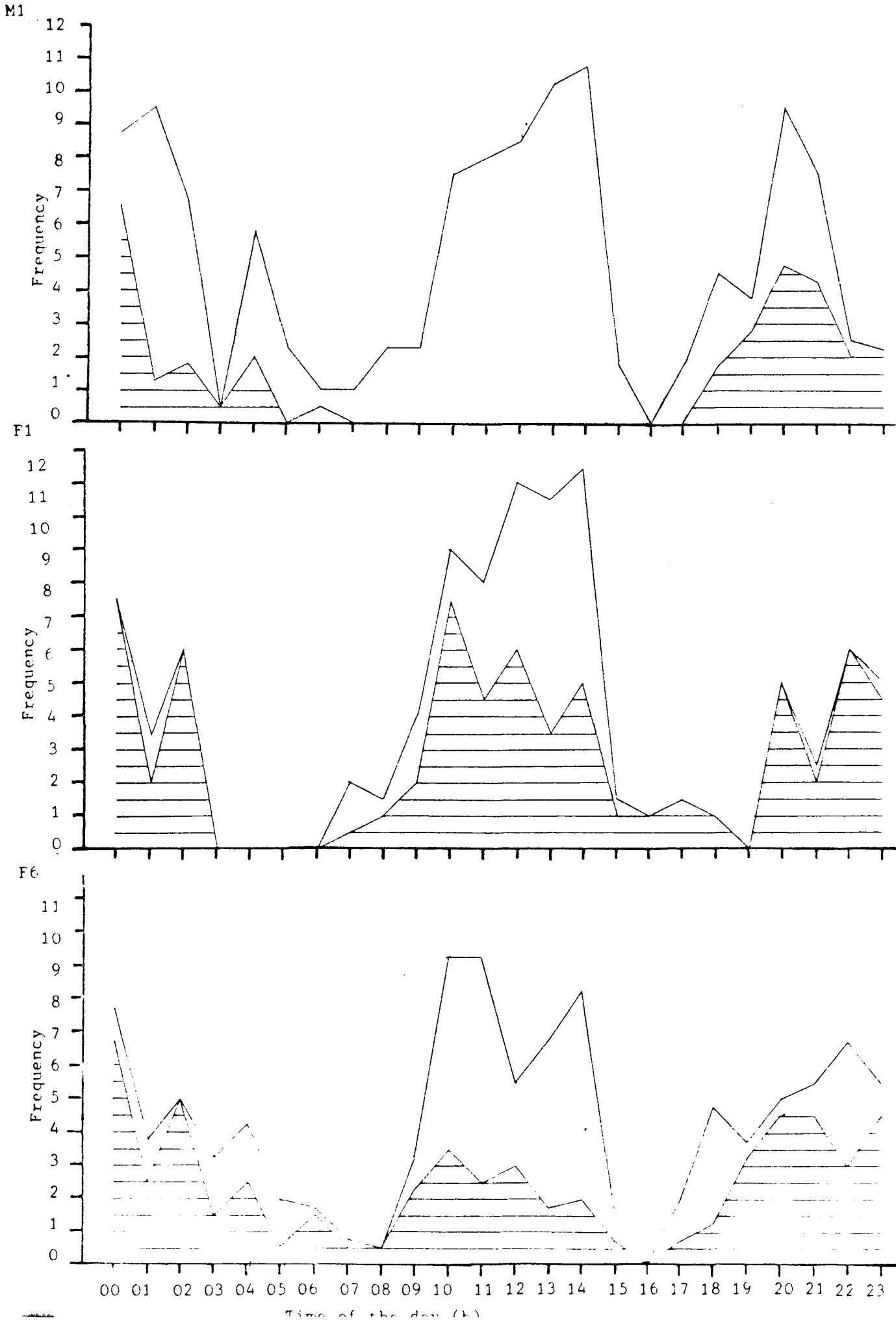

Frequency
Frequency
Frequency
Frequency
0
2
4
6
8
10
12
14
16
18
20
22
24

FIGURE 3.3.3: Mean frequencies of resting of three subjects showing the proportion of time spent resting with another (hatched area). Sample-days used as replicates; n=4 for M1 and F1, n=2 for F6.


M1
F1
F6
Frequency
0 1 2 3 4 5 6 7 8 9 10 11 12
00 01 02 03 04 05 06 07 08 09 10 11 12 13 14 15 16 17 18 19 20 21 22 23
Time of the day (h)

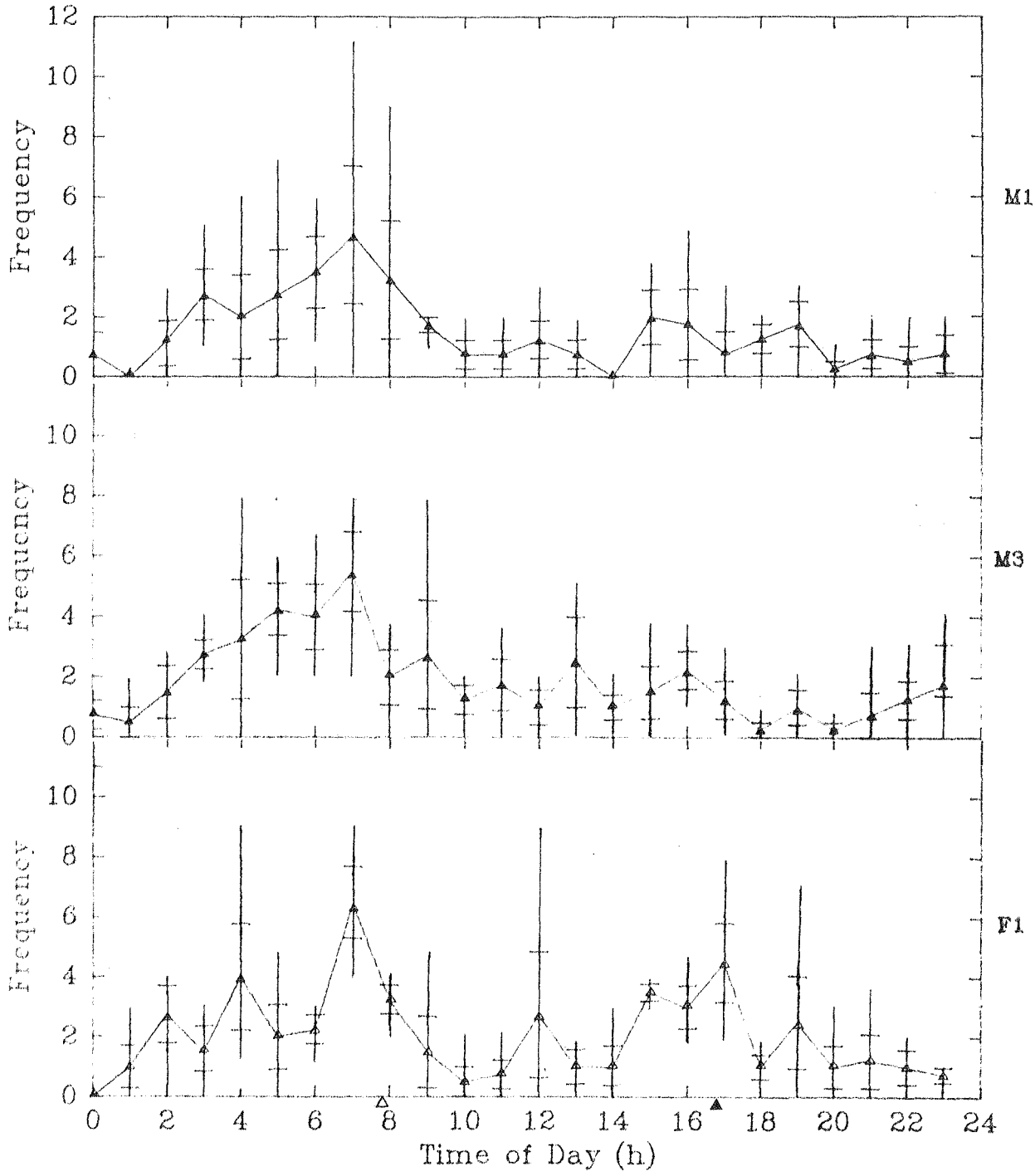
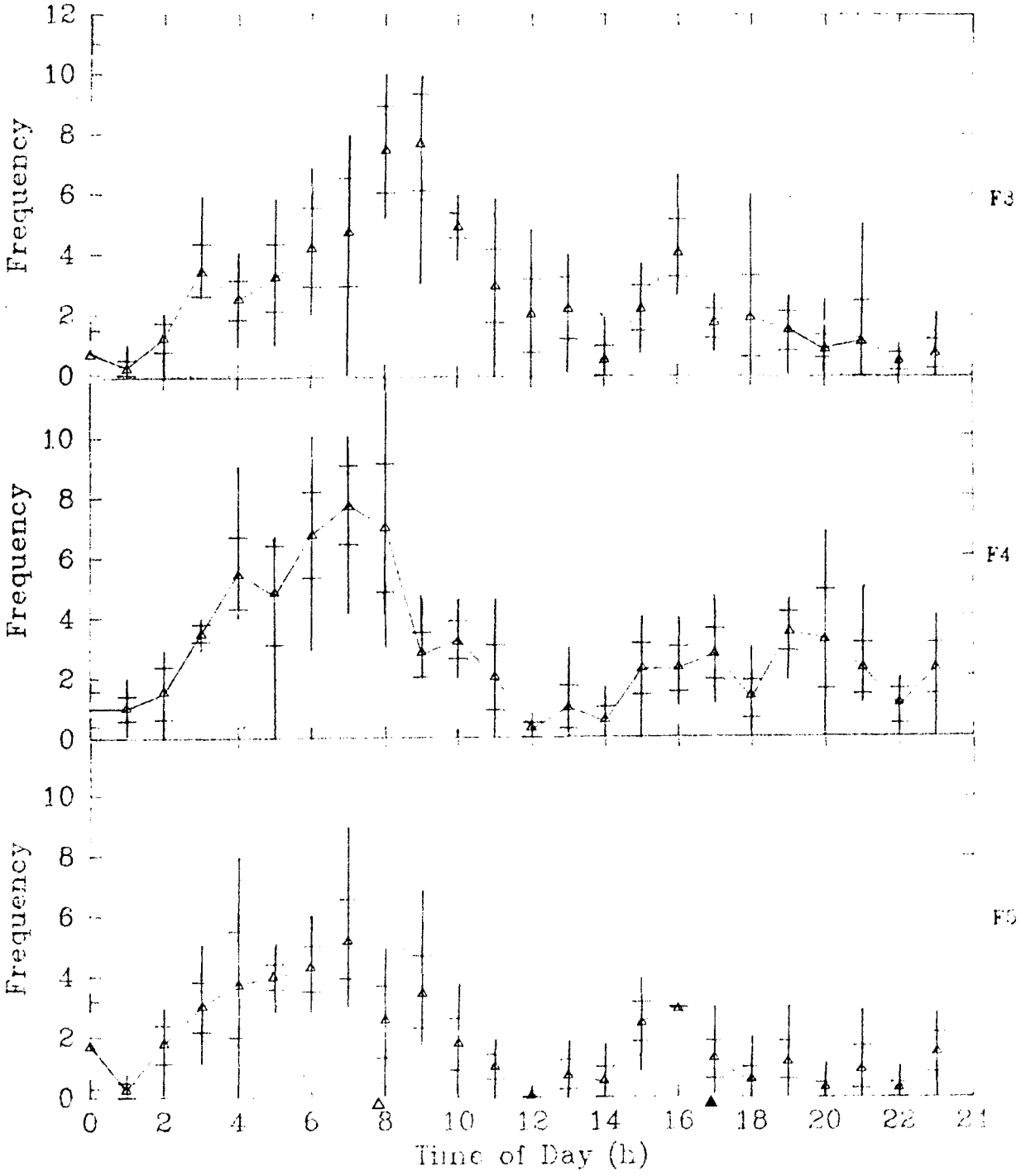


FIGURE 3.3.4: Mean, standard error and range of standing scores of the four sample-days for the six subjects.

△ mean time of sunrise

▲ mean time of sunset


Frequency
F3
F4
F5
Time of Day (h)

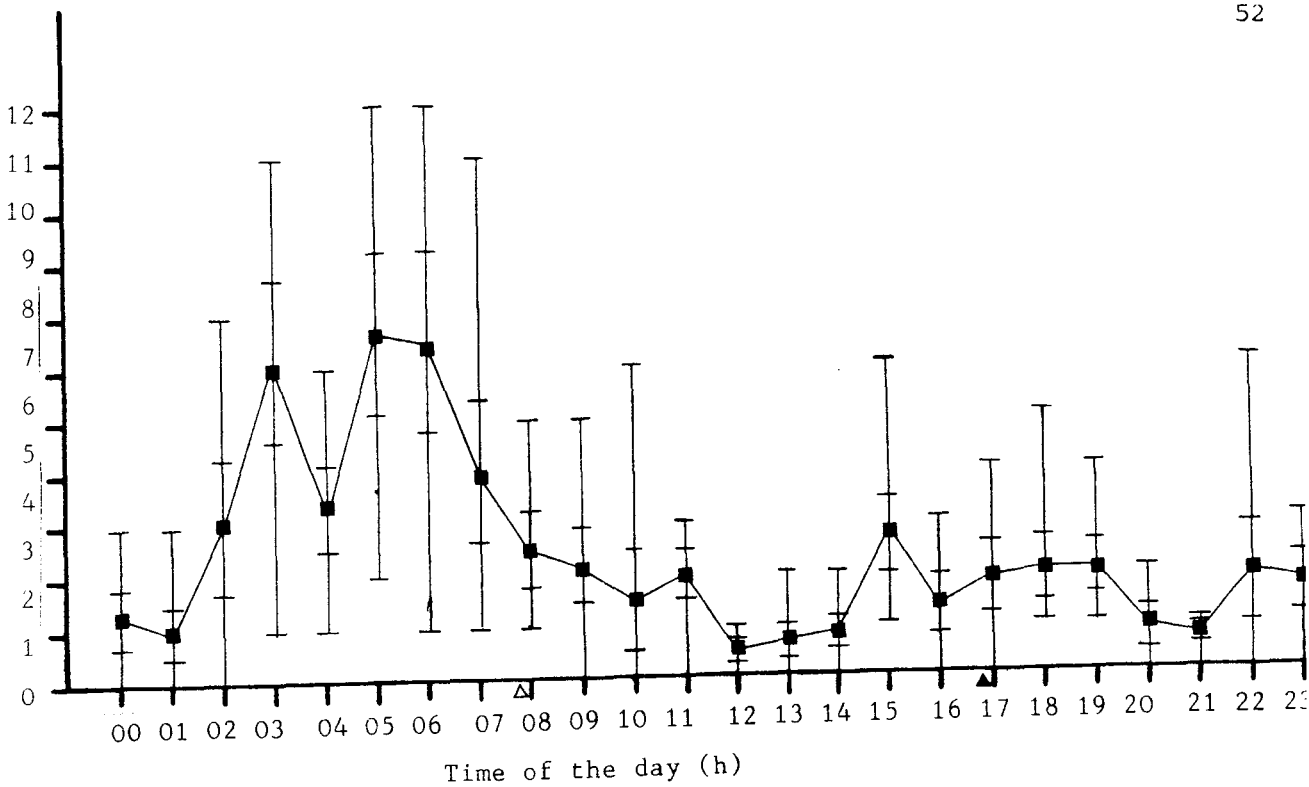


FIGURE 3.3.5: Mean, standard error and range of locomotor scores (totaled for the four sample days) of the six subjects (n.b. The maximun score for each subject during any hour sample is 48).

△ mean time of sunrise (for total study period)

▲ mean time of sunset "

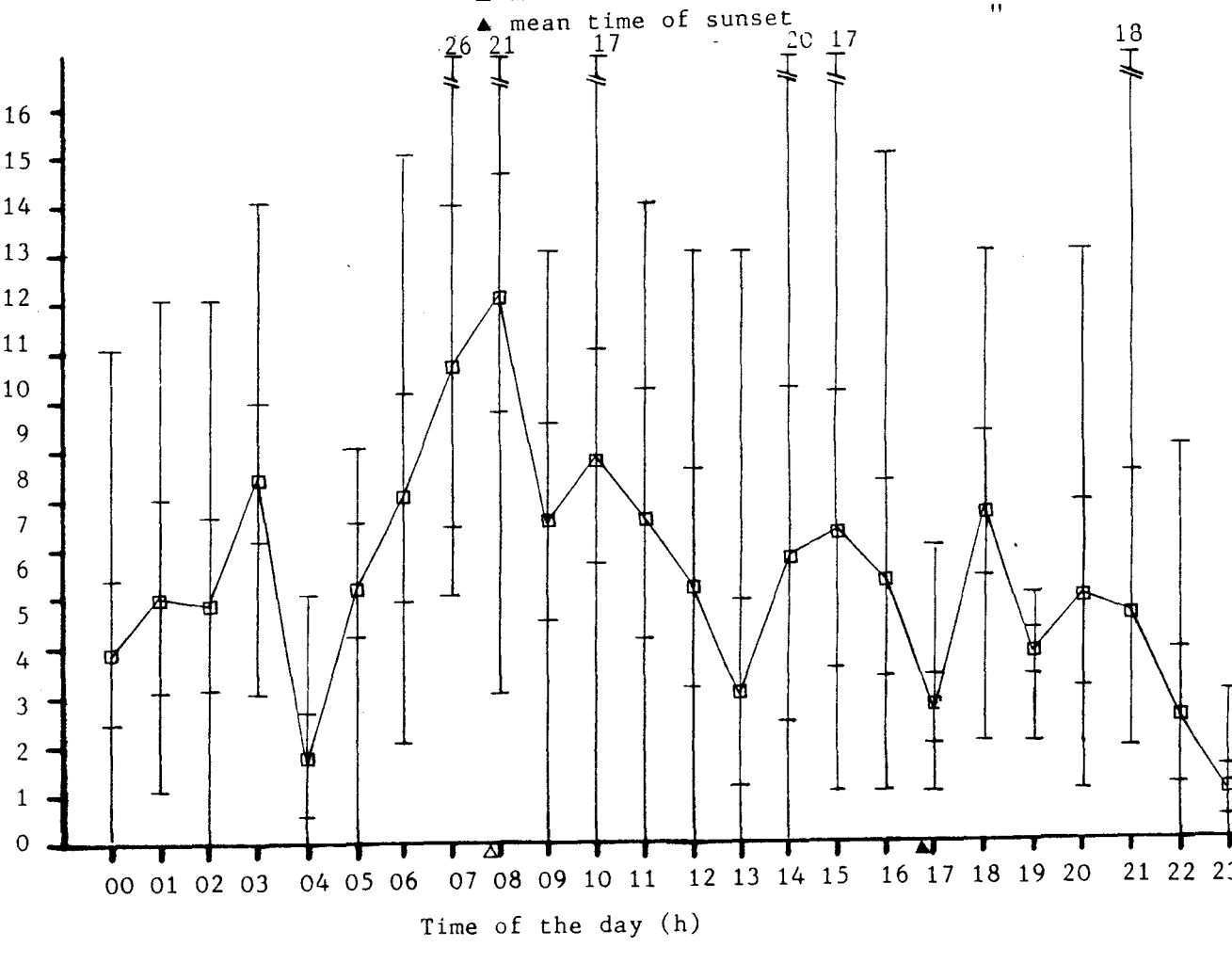


FIGURE 3.3.6: Mean, standard error and range of scores when subjects (n=6) were not visible (scores of each subject totaled for the four sample-days).

△ mean time of sunrise

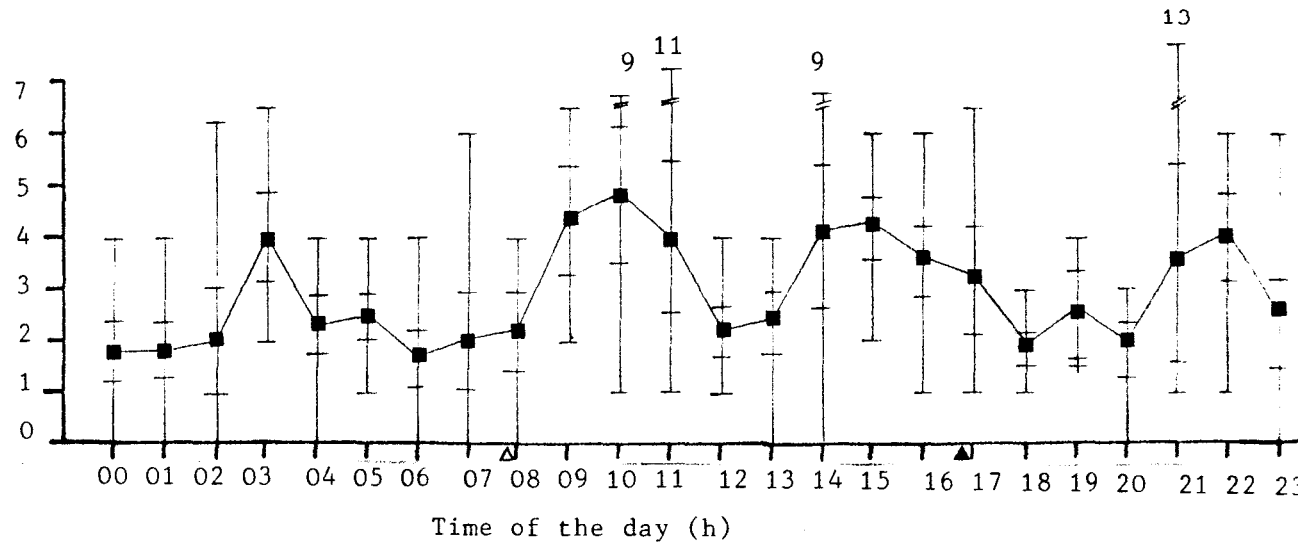


FIGURE 3.3.7: Mean, standard error and range of autogrooming scores (totaled for the four sample-days) of the six **subjects.** Pouch grooming omitted from female scores.
△ mean time of sunrise
▲ mean time of sunset

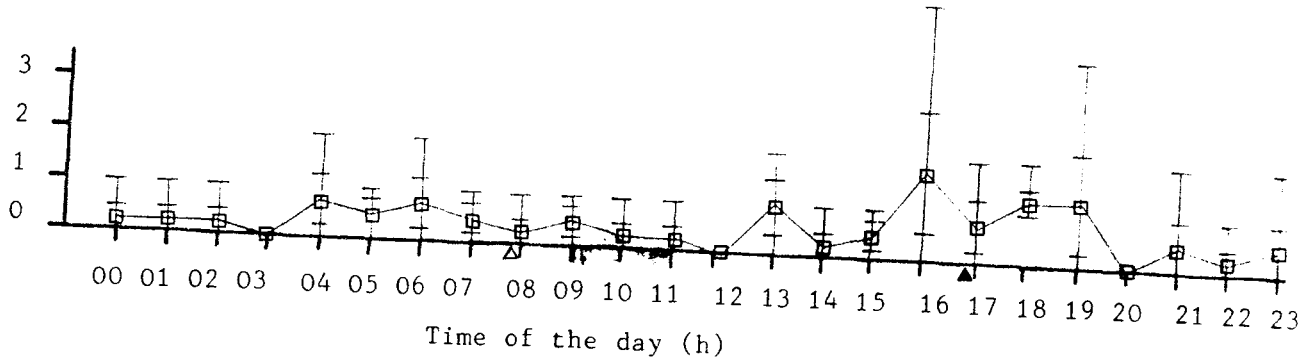


FIGURE 3.3.8: Mean, standard error and range of scores of pouch grooming (totaled for the four sample-days)of the female subjects (n=6).
△ mean time of sunrise
▲ mean time of sunset

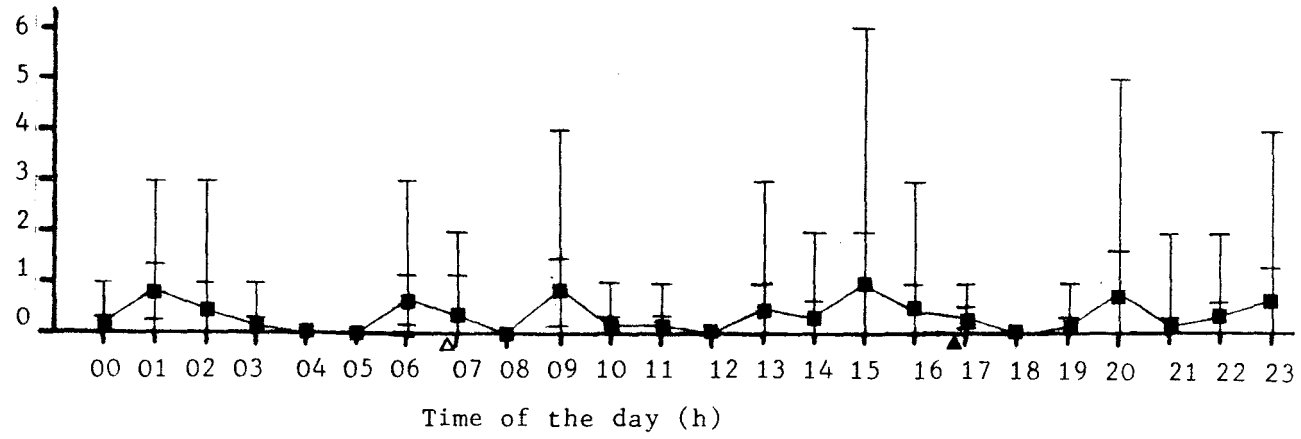


FIGURE 3.3.9: Mean, standard error and range of allogrooming scores (totaled for the four sample-days) of the six subjects.
△ mean time of sunrise
▲ mean time of sunset

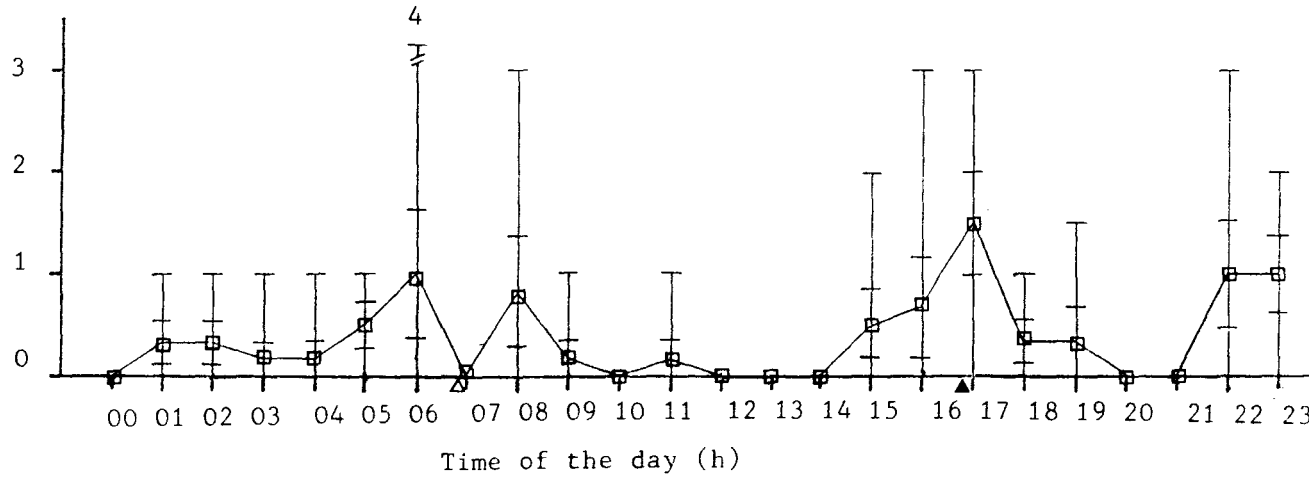


FIGURE 3.3.10: Mean, standard error and range of drinking scores (totaled for the four sample-days) of six subjects.
△ mean time of sunrise
▲ mean time of sunset

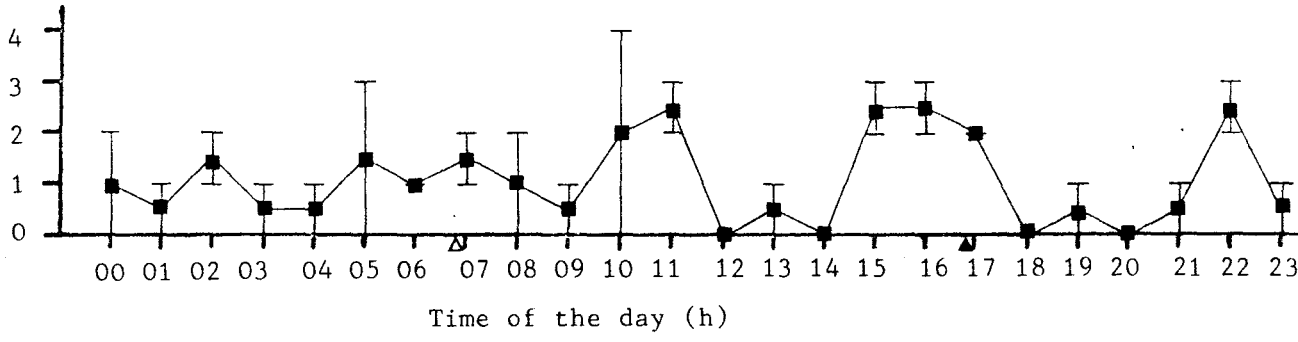


FIGURE 3.3.11: Mean, standard error and range of scores of sexual interactions (totaled for the four sample-days) of male subjects (n=2).
△ mean time of sunrise
▲ mean time of sunset

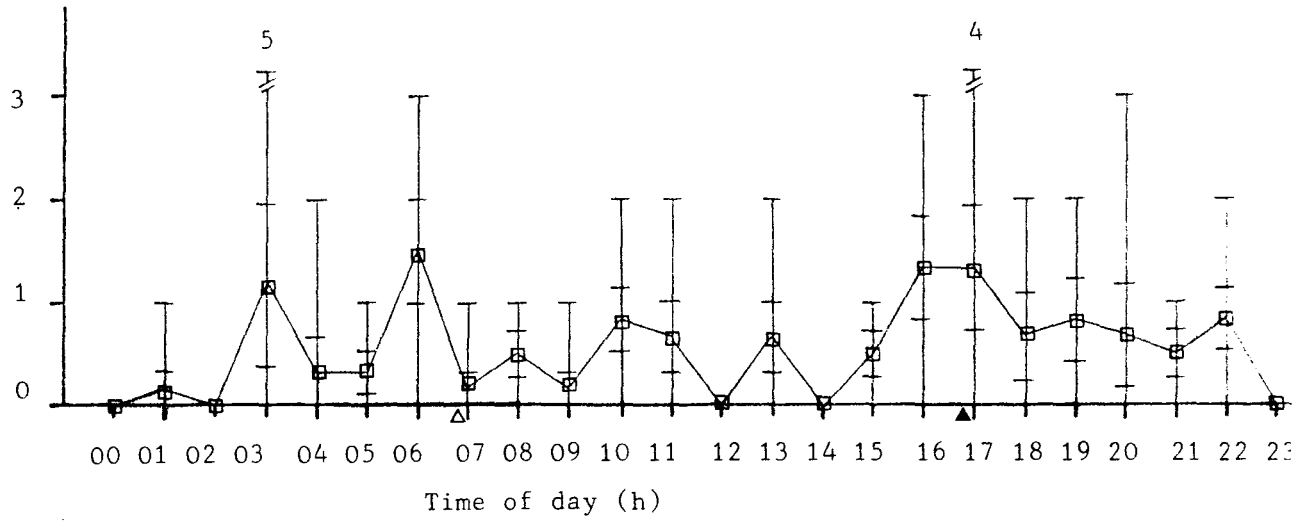


FIGURE 3.3.12: Mean, standard error and range of scores of non-sexual interactions (totaled for the four sample-days) of the six subjects.
△ mean time of sunrise
▲ mean time of sunset

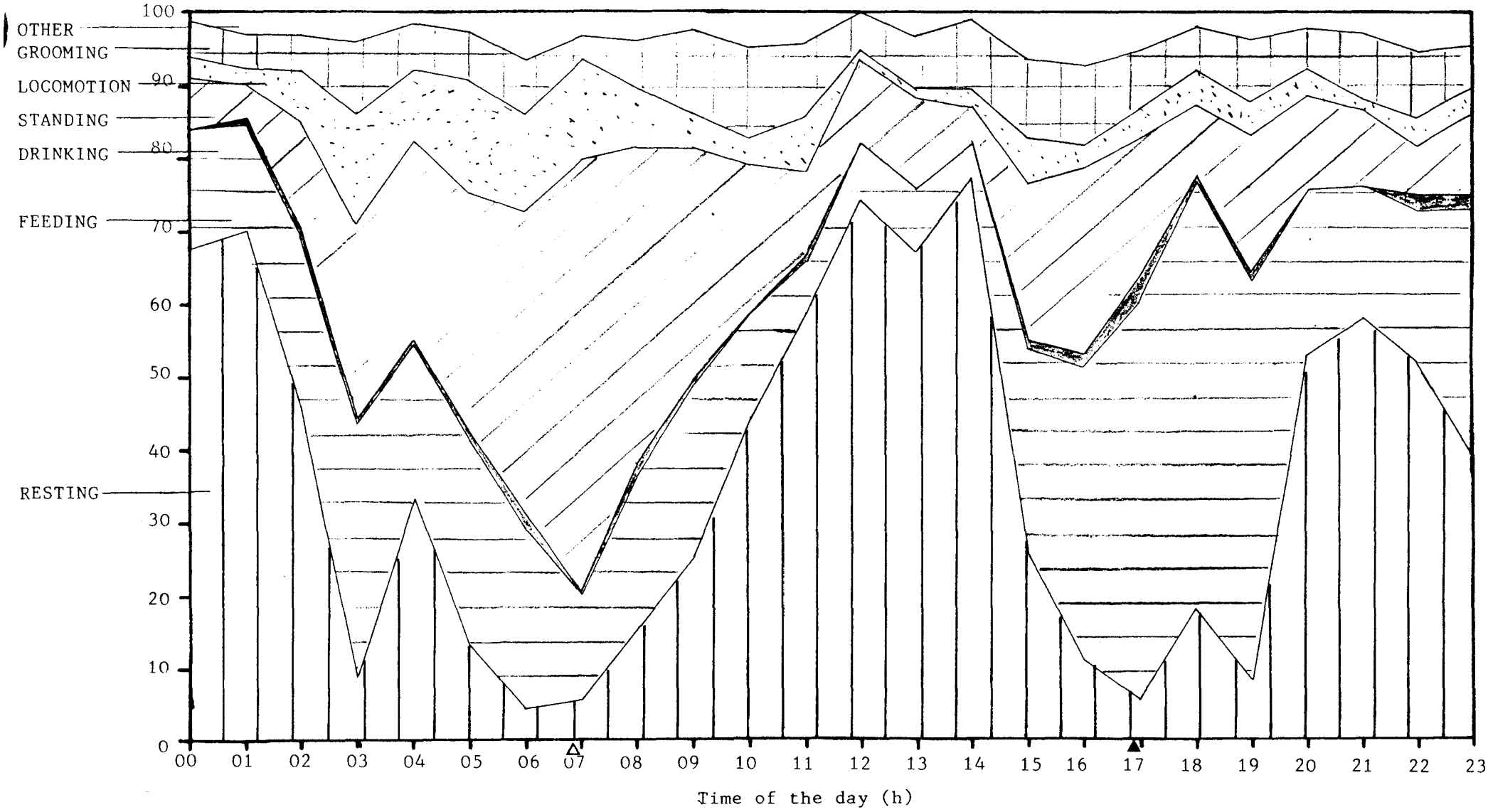


FIGURE 3.3.13: A general diel activity-cycle for captive subjects of *Thylogale billardierii* (n=6) based on the percentage time engaged in each activity.

TABLE 3.3.16 Resting positions of individual subjects of *Thylogale billardierri* within the enclosure. The positions were tabulated as grid references (see Figure 2.1). Numbers in brackets are the numbers of grid squares used (np) and the total numbers of observational samples (n) respectively.

	Time of Day			
	0615h - 1810h		1815h - 0610 h	
Animal	Position	% Time	Position	% Time
M1	D4	64	A1	40
	D4P	25	B1	23
			C2	18
	(np=8)	(n=226)	(np=8)	(n=240)
F1	B1P	36	A1	48
	D1P	17	B1	25
	G1P	16		
	(np=12)	(n=197)	(np=9)	(n=227)
F6	D4	47	A1	69
	B1P	27	B1	24
	(np=7)	(n=156)	(np=3)	(n=115)
F5	D4	49	A1	29
	G1P	38	D4P	26
			A2	12
			C2	11
	(np=5)	(n=136)	(np=12)	(n=227)
F4	D3	46	C2	33
	D4	35	B3	17
			B2	13
			D4P	10
	(np=6)	(n=136)	(np=9)	(n=145)
M3	D4	58	C2	38
	C1	10	A1	21
			B1	14
			A2	11
	(np = 8)	(n = 175)	(np=11)	(n=175)
F3	D3	31	B1	40
	D1	27	C2	24
	C1P	13	A1	20
	G1	11		
	(np=8)	(n=187)	(np=7)	(n=254)

within grid squares, it was noted that animals often showed high fidelity to specific locations inside given grid squares.

Analysis of the spatial distribution of resting, locomotion and standing positions were made based on the hypothesis that these occur randomly within the enclosure, with respect to the central and peripheral regions. χ^2 test values for each subject are shown in Tables 3.3.17, 3.3.18 and 3.3.19, for each of the three behavioural categories considered. Expected frequencies were calculated on the presumption that utilization of each region was proportional to its relative area (the peripheral region constituted 14% of the total area of the enclosure).

There was a marked peripheralization of locomotion (Table 3.3.18) in all subjects except M1, F1 and F6, corresponding to regular fence-running behaviour exhibited by these animals (M3, F3, F4, F5). The same trend is shown in the distribution of scores of standing behaviour (Table 3.3.19) however, M1, F1 and F6 also exhibited peripheralization in 0615h-1810h period in all cases, significant centralization or perhiperalization of scores of resting behaviour may be attributed to individual subject's preference for certain resting-places. Data obtained for F6 are from the second half of the total observation period only.

3.3.3 Time-Budgets

Table 3.3.20 shows estimates of the amounts of time per day individual subjects spent engaging in each of the behavioural categories, based on the total number of scan samples recorded over the sample-period. Scores when subjects were not visible were not eliminated. This would have introduced substantial errors in the estimates because individual subjects were unsighted for unequal periods of time (Table 3.3.9). Furthermore, the only source of water within the enclosure was in clear view, as was the food hopper (although subjects fed at all points of the enclosure), hence over-estimates of amounts of times spent drinking or feeding would resuult.As F6 was out of the pouch for only a half of the total sampling-

TABLE 3.3.17 Observed frequencies of resting positions in central and peripheral regions of enclosure for individual subjects of *Thylogale billardierii*. Expected frequencies shown in brackets.

Animal	Time of Day	Central	Peripheral	Total	χ^2(df = 1)	Probability
M1	0615h-1810h	70 (194.36)	156 (31.64)	226	568.4	<0.001
	1815h-0610h	233 (206.40)	7 (33.60)	240	24.5	<0.001
M3	0615h-1810h	146 (150.50)	29 (24.50)	175	0.96	n.s.
	1815h-0610h	175 (150.50)	0 (24.50)	175	28.5	<0.001
F1	0615h-1810h	42 (169.42)	155 (27.58)	197	684.5	<0.001
	1815h-0610h	221 (195.22)	6 (31.78)	227	24.3	<0.001
F3	0615h-1810h	163 (160.82)	24 (26.18)	187	0.21	n.s.
	1815h-0610h	251 (218.44)	1 (35.56)	252	38.7	<0.001
F4	0615h-1810h	135 (116.96)	1 (19.04)	136	19.9	<0.001
	1815h-0610h	130 (124.70)	15 (20.30)	145	1.60	n.s.
F5	0615h-1810h	78 (116.96)	58 (19.04)	136	92.7	<0.001
	1815h-0610h	169 (195.22)	58 (31.78)	227	25.2	<0.001
F6	0615h-1810h	92 (134.16)	64 (21.84)	156	94.6	<0.001
	1815h-0610h	115 (98.90)	0 (16.10)	115	18.7	<0.001

TABLE 3.3.18 Observed frequencies of locomotion positions in central and peripheral regions of enclosure for individual subjects of *Thylogale billardierii*. Expected frequencies shown in brackets.

Animal	Time of Day	Central	Peripheral	Total	χ^2(df = 1)	Probability
M1	0615h-1810h	18 (18.92)	4 (3.08)	22	0.32	n.s.
	1815h-0610h	10 (10.32)	1 (1.54)	11	0.07	n.s.
M3	0615h-1810h	15 (19.78)	8 (3.22)	23	8.25	<0.01
	1815h-0610h	26 (41.28)	22 (6.72)	48	40.40	<0.001
F1	0615h-1810h	15 (15.48)	3 (2.52)	18	0.11	n.s.
	1815h-0610h	10 (10.32)	2 (1.68)	12	0.07	n.s.
F3	0615h-1810h	11 (19.78)	12 (3.22)	23	27.84	<0.001
	1815h-0610h	17 (36.98)	26 (6.02)	43	77.11	<0.001
F4	0615h-1810h	21 (26.67)	10 (4.33)	31	8.58	<0.01
	1815h-0610h	18 (30.1)	17 (49)	35	34.74	<0.001
F5	0615h-1810h	19 (31.82)	18 (5.18)	37	36.89	<0.001
	1815h-0610h	11 (31.82)	26 (5.18)	37	97.30	<0.001
F6	0615h-1810h	21 (23.22)	6 (3.78)	27	1.52	n.s.
	1815h-0610h	17 (15.48)	1 (2.52)	18	1.07	n.s.

TABLE 3.3.19 Observed frequencies of standing positions in central and peripheral regions of enclosure for individual subjects of *Thylogale billardierii*. Expected frequencies shown in brackets.

Animal	Time of Day	Central	Peripheral	Total	χ^2(df = 1)	Probability
M1	0615h-1810h	56 (67.94)	23 (11.06)	79	14.99	<0.001
	1815h-0610h	48 (48.16)	8 (7.84)	56	0.00	n.s.
M3	0615h-1810h	70 (88.58)	33 (14.42)	103	27.84	<0.001
	1815h-0615h	43 (65.36)	33 (10.64)	76	54.64	<0.001
F1	0165h-1810h	76 (99.76)	40 (16.24)	116	40.42	<0.001
	1815h-0610h	58 (57.62)	9 (9.38)	67	0.02	n.s.
F3	0615h-1810h	141 (152.22)	36 (24.78)	177	5.91	<0.05
	1815h-0610h	52 (65.36)	24 (10.64)	76	19.51	<0.001
F4	0615h-1810h	103 (123.74)	41 (20.16)	144	25.05	<0.001
	1815h-0610h	83 (111.80)	47 (18.20)	130	52.99	<0.001
F5	0615h-1810h	61 (92.88)	47 (15.12)	108	78.16	<0.001
	1815h-0610h	46 (66.22)	37 (10.78)	77	44.10	<0.001
F6	0615h-1810h	39 (51.60)	21 (8.40)	50	21.98	<0.001
	1815h-0610h	59 (63.64)	15 (10.36)	74	2.42	n.s.

TABLE 3.3.20 Estimated time budgets for captive individuals of *Thylomale billardierii*.

Animal	Feeding	Drinking	Resting: Alone	Resting: With Another	Resting: Total	Grooming: Auto	Grooming: Pouch	Grooming: Allo	Standing	Sexual Interaction	Other Interaction	Locomotion	Other	Not Visible
M1	5h40min	21.25min	7h30min	2h27.5min	9h57.5min	1h45min	-	17.5min	2h46.25min	32.5min	26.25min	43.75min	6.25min	1h23.75min
M3	5h21.25min	11.25min	7h27.5min	0	7h17.5min	1h16.25min	-	0	3h45min	35.0min	25.0min	1h27.5min	3.25min	3h37.5min
F1	4h51.25min	7.50min	8h53.75min	4h53.75min	8h47.5min	1h41.25min	32.5min	46.75min	4h7.5min	-	11.25min	37.5min	2.5min	2h13.5min
F3	3h23.75min	12.50min	9h13.75min	0	9h13.75min	59.75min	7.5min	0	5h17.5min	-	8.25min	1h10.75min	0	2h10.75min
F4	5h22.5min	9.25min	6h15min	0	6h45min	1h35min	6.25min	0	5h43.75min	-	11.25min	1h27.5min	1.25min	3h38.75min
F5	6h15min	6.25min	7h11.25min	20min	7h31.25min	1h20min	16.25min	0	3h51.25min	-	16.25min	1h32.5min	2.5min	2h58.75min
TOTAL	5h21.67min	11.46min	6h27.7min	1h16.88min	7h54.58min	1h37.5min	15.63min	10.71min	4h19.79min	15.61min	16.46min	1h11.67min	3.54min	2h40.42min

TABLE 3.3.21 Estimated time budgets for one young *Thylogale billardierii* for each of the four sample-days.

Sample-day	In Pouch: Completely	In Pouch: Head out	Head out, feeding	Feeding	Resting: Alone	Resting: With Other	Resting: Total	Standing	Locomotion	Grooming: Auto	Grooming: Allo	Grooming: Pouch	Sucking	Drinking	Interacting	Other	Not Visible
1	13h15min	3h20min	40min	5min	0	0	0	1h	40min	5min	5min	0	40min	0	0	0	3h50min
2	3h15min	11h5min	0min	2h15min	1h20min	3h55min	5h	3h15min	45min	25min	1h25min	0	1h10min	0	0	10min	4h15min
3	"	"	"	2h15min	1h55min	3h10min	10h5min	3h40min	55min	1h5min	10min	5min	15min	0	10min	0	2h55min
4	"	"	"	3h45min	2h40min	5h25min	8h5min	4h10min	1h55min	1h35min	25min	0	20min	5min	0	10min	2h30min

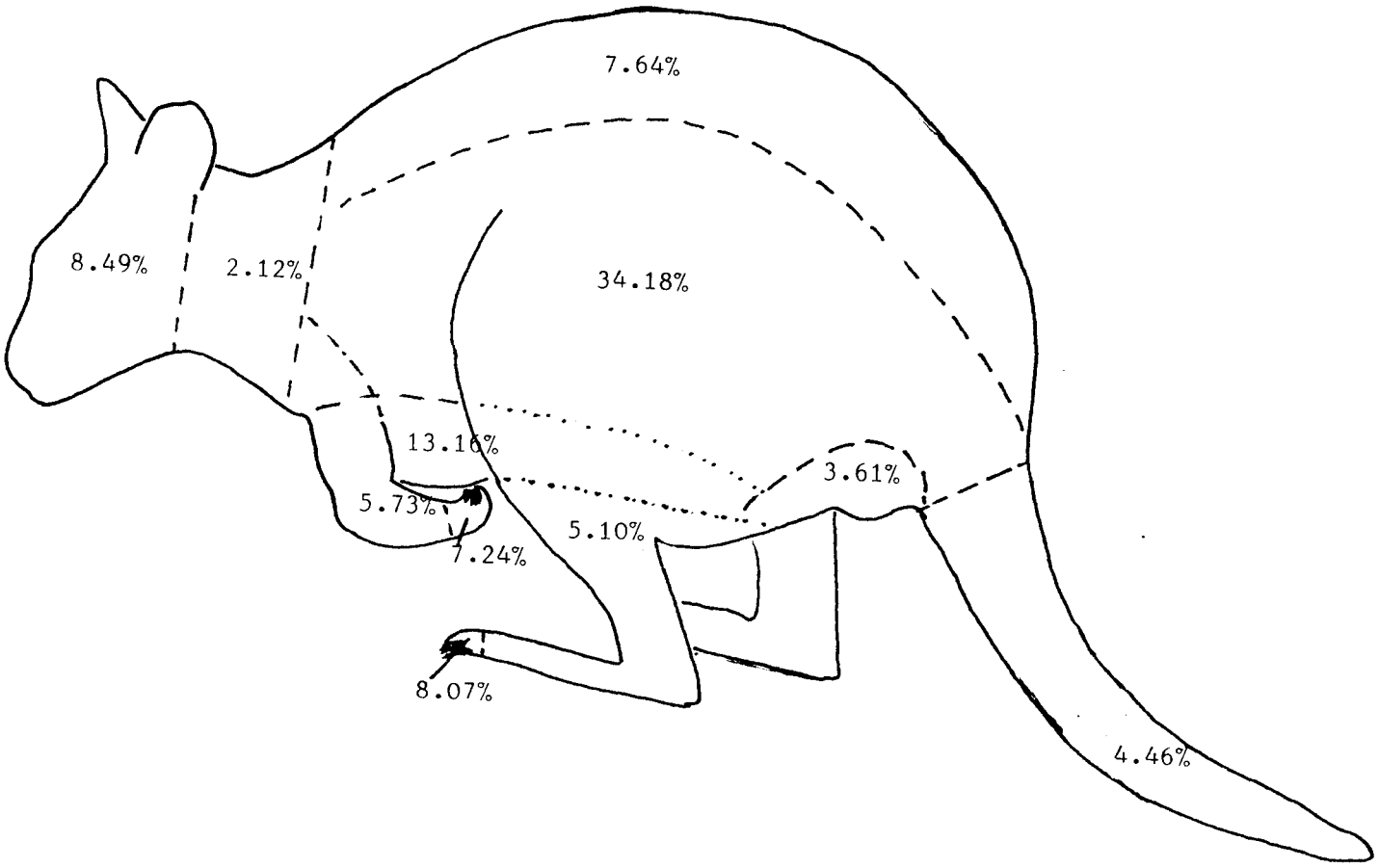


FIGURE 3.3.14: The percentage of grooming activities devoted to each sector of the body. Grooming of the pouch area omitted from female grooming scores.(n=6)

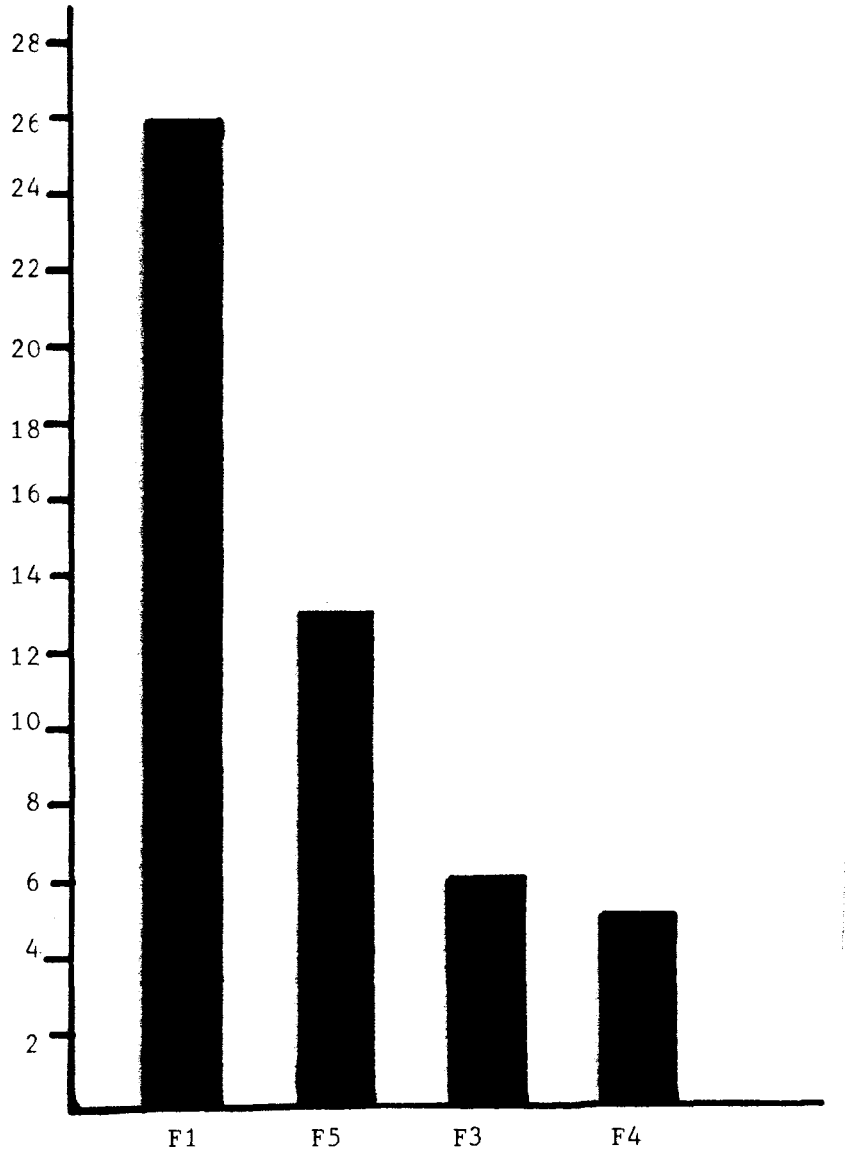


FIGURE 3.3.15: The total scores of pouch grooming of each female subject (n=4) for the entire study period i.e.96h

period, she is considered separately (Table 3.3.21).

The broad category termed "other" behaviours included standing "full-stretch", regurgitation and sniffing at the observer's hide.

The distribution of grooming of various parts of the body are shown in Figure 3.3.14. There was no significant difference with respect to these activities between males (n = 2) and females (n = 4) based on tests using a contingency χ^2 table (χ^2_7 = 3.22 *fe* <2 = 0, percentage of *fe* <5 = 31). Observed frequencies for both sexes were each divided by their respective number of individuals so as to enable them to be directly comparable. Sectors of the body with low observed frequencies were combined to validate the analysis. Pouch grooming by females was excluded from this analysis (Tables 3.3.10 and 3.3.11). The frequencies of pouch grooming recorded for each female subject are shown in Figure 3.3.15.

3.4 DISCUSSION

The results show that captive *T. billardierii* exhibit certain regularities in their diel behaviour. However, they are to some extent labile with respect to their activity patterns. There were no significant differences in the frequencies of recorded activities between the four sample-days. The time limitations of this study precluded the possibility of investigating seasonal influences. Seasonal variations in the frequencies of occurrence of certain behaviours have been demonstrated in *Macropus rufus* (Croft 1981a), *M. robustus erubescens* (Croft 1981b), *M. parryi* (Kaufmann 1974a). *Thylogale thetis* (Johnson 1980) and *Setonix brachyurus* (Packer 1965; Nicholls 1971).

Most commonly, changes in activity-patterns are attributed to changes in daylength and climatic conditions such as variations in ambient temperature. Biotic factors, especially changes in the distributions and abundance of food items and the influence of predator species, are often also important.

There were significant variations between the frequencies for hours of the day of each of the categories feeding, resting and standing over the four sample days (Tables 3.3.2, 3.3.4 and 3.3.6), indicating short-term changes in the distribution of observed frequencies of these categories over the sample period (Figures 3.3.1 and 3.3.2). The initial shortening and subsequent lengthening of periods of daylight over the course of the study may account for some of these modulations (Table 3.3.1); however, other factors must also be involved.

The acquisition of an improved observation room subsequently to this phase of the study permitted observations to be performed in very heavy rain; however no quantitative study of this was undertaken. During heavy rain, subjects periodically adopted the semi-upright posture described by Morton and Burton (1973), but the animals also were observed to continue feeding and moving about in the open sectors of the enclosure even in periods of extremely copious rainfall. Casual observations during a period of light snowfall disclosed no overt effects on the behaviour of the subjects.

3.4.1 Feeding and Drinking

There were no significant differences in the amounts of feeding activity recorded either between or within groups of subjects (Table 3.3.3). It may be expected that females with pouch young would require a greater intake of food to compensate for the energy demands of lactation. The body weight of neonatal *T. billardierii* increases only by *ca.* 100 g in the first twenty weeks of pouch-life and up until this stage the presence of the young would presumably exert little nutritional strain on their mothers; however, in the subsequent ten weeks the developing young gain up to 1 kg in weight (Rose and McCartney 1982b).

Subject F1 lost 16% of her body weight over the period of F6's pouch-life whilst F5 gained 17.4% in her body weight during M4 pouch-life (Appendix 1.1). Although accurate ageing was not possible, F5 was most

probably a young individual. F5 also fed for the longest period of time (Table 3.3.20). McCartney (1978) reported a loss of 20% in weight in one female *T. billardierii* and large fluctuations of weight in another over the period of their offspring's pouch-life.

Efficiency of the digestion of food materials may differ between individuals. Rates of the passage of food through the stomach was found to be retarded, thus increasing the utilization of cellulose, in *M. rufa, M. giganteus, S. brachyurus* and *Ovis aries* (Artiodactyla:Bovidae) when the animals were provided with a subsistence diet (Tyndale-Biscoe 1973). In macropods this is achieved by functionally changing the structural fold which are present in forestomach wall (Langer 1979b; Langer *et al.* 1980). *T. thetis* and *T. stigmatica* both have relatively large saccular regions of the forestomach which enables them to cope with varying quantities of food but not with food of low quality (Langer 1979a,b,c).

The morphology of the stomach of *T. billardierii* has not been investigated in detail. Johnson (1978) found no significant differences in the faecal output of three captive *T. billardierii* (1 adult male, 1 adult female, 1 subadult male) given a constant food supply. No studies have been performed to date on the effects of different quantities and qualities of food items, on feeding and digestive strategies of *T. billardierii,* nor of the effects of factors such as age, sex, presence of pouch young, by any previous investigators.

The recorded frequencies of feeding in captive subjects achieved a peak at sunset, with secondary, less well-defined peaks of this activity occurring late at night and in the early morning (Figure 3.3.1). In ruminants, the specialized routine of feeding/ruminating precludes the occurrence of long periods of inactivity, particularly deep sleep (Balch 1955) and ingestion of food is necessary at short intervals in order to maintain condition (Leuthold 1977).

Macropods possess a ruminant-like digestive system (Moir *et al.* 1956, Tyndale-Biscoe 1973). All of the subfamily Macropodinae, so far

investigated exhibit peaks of feeding behaviour at various times of the day (usually at dusk and dawn); however, feeding behaviour occurs, albeit at lower frequencies, throughout most of the day. In the subfamily Potorinae, long rest periods appear to be the norm (*Bettongia lesueuri*, Stodart 1966; *B. gaimardi*, Johnson 1978, Rose *pers. comm,; Aepyprymnus rufescens*, Johnson 1980b; *Potorous tridactylus apicalis* Buchmann *pers. comm.*) possibly corresponding to their more catholic diet.

Johnson (1978) found that *T. billardierii* moved into pastures after sunset and remained there until just before dawn (Figure 3.4.1).

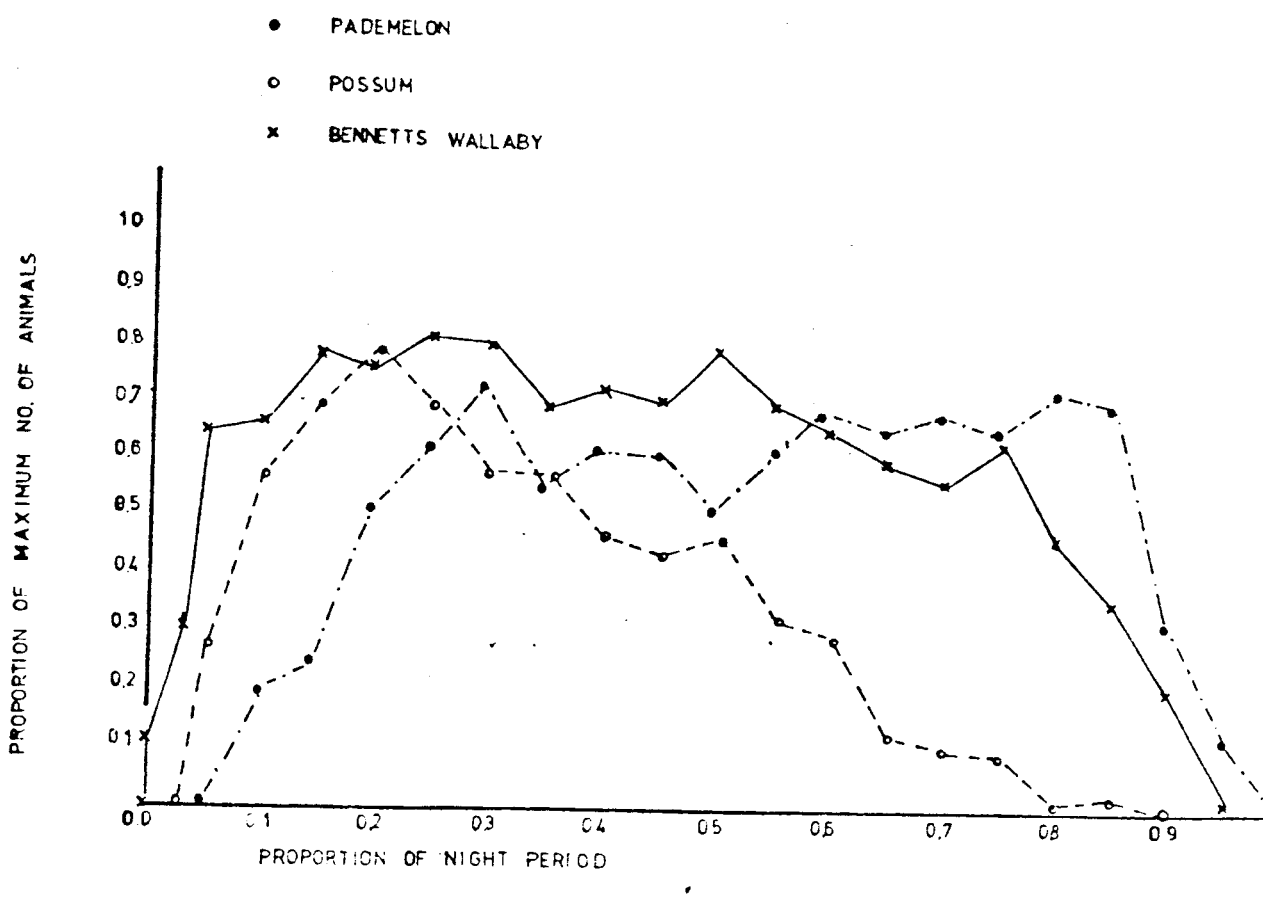


FIGURE 3.4.1: Proportional representation of the numbers of bennetts wallaby, pademelon and brush possum counted at portions of the sunset to sunrise period. (after Johnson 1978)

Radio-tracked *T. billardierii* moved quickly from their daytime resting locations to their feeding areas at dusk. No record of the behaviour of *T. billardierii* whilst present in pasture, was presented by the author, consequently whether the peaks in feeding observed in this study are typical or not, cannot be stated.

Johnson's (1978) study area was situated in a dry sclerophyll forest, traversed by moist gullies bordered by dense vegetation which *T. billardierri* utilized for cover during the day. Members of the genus *Thylogale* generally appear to be adapted to relatively humid habitats (Langer 1979b) and in the exploitation of this heterogeneous habitat by *T. billardierii*, certain restrictions may be placed on their activity-patterns.

T. billardierii are categorized as browsers on the basis of their dentition by Sanson (1978) and have been noted to supplement their diet of green grasses and herbs by browse from taller dicotyledons (Johnson and Rose, in press). It is therefore probable that animals feed during the day in the gullies, which Johnson (1978) designated as resting places.

The significant variations between the frequencies for hours of the day of feeding by individual subjects (Table 3.3.3), indicates individuals tend to feed at different times to each other. This is probably related to the social structure of the animals (Section 5.3.1). For example, higher-ranking individuals fed at the food hopper, to the exclusion of subordinates.

There was no significant difference in the recorded frequencies of drinking between individual subjects. Scores of "drinking" behaviour were recorded when a subject had its head in the water container. Therefore this is not a measure of the actual quantity of water ingested which may well have been different between individuals. The higher recorded frequencies of drinking, in general, corresponded to times of the day when the frequency of feeding was also high (Figure 3.3.10).

3.4.2 Resting

Resting was the predominant activity of the subjects at midday and generally two peaks of this category of behaviour were evident during the night (Figure 3.3.4). There appeared to be an inverse correlation between the incidences of resting and feeding. This is hardly surprising in view of the fact that they were mutually exclusive and constituted a high proportion of the diel activity periods.

Significant differences between the frequencies of resting of the individual subjects may not, in fact, yield realistic results because of the preference of individual subjects for certain specific resting-locations. If such a site was not within the field of vision of the observer, the resting behaviour of the subject associated with it would have provided conservative estimates of this activity. In this context, it should be noted that the subjects yielding the lowest scores for resting were also visible for the least amounts of time during the observation periods (Table 3.3.20).

It must be emphasised that in this study the occurrence of resting postures but not of sleep was scored. Animals were occasionally observed to sleep whilst in the "seated-down" position; however, this was not always the case, especially during the day (Section 2.3).

The observed dichotomy between day and night locations of resting (Table 3.3.16) is similar in some respects to the behaviour of *T. billardierri* studied in natural conditions (Johnson 1978). In general, the daytime preferred resting locations occurred in the regions of the enclosure containing the densest vegetation, whereas those used at night were distributed around the open regions of the enclosure (Figure 2.1).

There was also an apparent dichotomy in the diel resting behaviour of those individuals that rested together (Section 2.3), as shown in Figure 3.3.3. The reason for this is not clear. M1 was recorded as frequently resting with F5 during the day in the phase of the study

preceding the investigation described here. F1 and F5 were the only females with which M1 regularly rested. There is some evidence this behaviour is related to sexual courting (Section 4.4.3).

The frequency of social interactions is often markedly increased in captive animals (Leuthold 1977). This may be the case with this behaviour or it may even constitute a behavioural artifact of captivity as it has never been reported in free-living *T. billardierii*, nor in any other species of the Macropodinae, although it is of common occurrence in the Potoroinae. By contrast, the resting together of mother and offspring is probably a normal phenomenon and is discussed in Chapter 6.

Resting accounted for *ca.* one-third of the time budget of *T. billardierri* in captivity. As no quantitative diel investigation of resting behaviour have been presented for any species of macropods, the relevance of this result to related observations is not possible.

3.4.3 Locomotion and Standing

The significant difference observed between subjects with respect to frequencies of locomotion may be attributed to the regular fence-running activity of certain individuals (Section 2.3). The predominance of fence-running in M3, F3, F4 and F5 is also indicated by the high level of peripheralization of locomotion in these subjects. The drive governing fence-running may be related to various motivational states. Hediger (1955) associates stereotyped movements (fence-running would be an example of this in the terms of his definition) in captive animals with various manifestations of boredom; however, these are usually expressed in older animals (the reverse of trend in these subjects) and those maintained in isolation. Fence-running could also be related to investigative behaviour, a desire to reach food-materials outside the enclosure, the dissipation of excess energy, or escape behaviour.

There was some evidence for the possible involvement of the latter factor in the present study. M1 and F1 exhibited fence-running behaviour

at frequencies substantially lower than those recorded in other subjects. This is shown by their non-significant level of peripheralization of locomotion (Table 3.3.18) and the lower general incidence of locomotion in these individuals (Table 3.3.20). M1 and F1 were also the highest-ranking individuals in the social hierarchy of the groups (Section 5.3). Subordinate animals are, presumably, subject to greater socially-induced stresses than dominant individuals, hence they may be more predisposed to exhibit escape-tendencies. Subsequently to this phase of the study, a male and female subject were introduced into the enclosure on different occasions (Section 5.2). During the initial few days after introduction, each of these animals engaged in fence-running with greatly increased frequencies in comparison with other subjects, and their own fence-running behaviour at later stages of the observations. The velocity of locomotion, and the extent of their movements along the fence-line, whilst involved in this activity, were also greatly increased during the period immediately following introduction.

Monosexual interactions between males were often interspersed with periods of fence-running by subordinate individuals (Section 5.4), possibly reflecting a high level of general excitation or arousal in these animals.

As the incidence of standing is related to fence-running (Section 2.3) it is not surprising that there was also conspicuous peripheralization of this activity (Table 3.3.19). Frequencies of standing were high in all subjects that engaged in overt fence-running (M3, F3, F4, F5) pre-dawn (Figure 3.3.4); due, no doubt, to the relationship between the two activities. The frequency of locomotion also exhibits a peak prior to sunrise (Figure 3.3.5). The frequency of standing was highest at dawn in all six subjects (Figure 3.3.4).

Animals tended to stand for varying periods before adopting the "seated down" (resting) posture. This may explain the peripheralization

of standing in M1, F1 and F6 during the 0615h-1810h period (Table 3.3.19) in view of the fact that the preferred resting locations used by these subjects were also peripheralized during the day (Tables 3.3.16 and 3.3.17).

The significant differences occurring in the frequency of standing between subjects (Table 3.3.7) is probably related to several factors, for example the different frequencies of fence-running, variations in the distribution of periods when individual subjects were out of view (Tables 3.3.9 and 3.3.20) and the generalized nature of this category of behaviour.

3.4.4 Autogrooming and Pouch-grooming

There were no significant differences between individual subjects with respect to frequencies of autogrooming (Table 3.3.10c) nor in the amount of time spent grooming the various regions of the body by males and females (Section 3.3.3), except when grooming of the pouch by females was included in their total grooming (Table 3.3.10a,b). The method of sampling employed was not conducive to the investigation of slight differences in behavioural events which may, nevertheless, be important in terms of the comfort of the animals.

Differences in grooming activities correlated with variations in temperature have been demonstrated in *M. rufus* (Russell 1971) and in *M. robustus* (Russell 1969). Certain types of grooming activities have become ritualized in the agonistic "displays" of larger macropods (Kaufmann 1974a; Grant 1974; Croft 1981a,b).

Pouch-grooming was clearly more frequently practised by female subjects that had pouch-young and there was also a clear trend for this activity to increase with increasing age of the pouch-young (Tables 3.3.10a, and 3.3.11, Figure 3.3.15), presumably associated with a corresponding increase in the rate of excretion by the infant.

Increases in the frequency of pouch-cleaning with the advent of birth,

followed by further increasing frequencies of this activity as the young grows have been reported in *M. rufus* (Frith and Calaby 1969; Russell 1970b), *M. giganteus* (Hermann 1967 after Russell and Giles 1974; Grant 1974), *M. eugenii* (Russell 1973; Russell and Giles 1974) and is also the general trend in the potoroine marsupial, *P. tridactactylus apicalis* (Buchmann *pers. comm.*).

In view of the small size of the pouch-young at the time of birth (weights of neonates in macropods range from 0.3 g to 0.85 g, McCartney 1978), it has been postulated that hormonal stimuli and the event of paturation are important factors governing the early increases in pouch-grooming (Russell and Giles 1974) whereas subsequently stimuli from the developing young become important.

There was no significant difference in autogrooming (pouch-grooming excluded) throughout the day (Table 3.3.10c), indicating that this activity was performed at a relatively constant diel level. Autogrooming was thus also associated with various other elements of behaviour in *T. billardierii*. There was some evidence of peaks of autogrooming preceding and following rest-periods (Figure 3.3.7).

There was a significant difference in the levels of pouch-grooming occurring at various times over the 24th period (Table 3.3.11) with there being an apparent peak *ca.* 1600h-1900h (Figure 3.3.8). The reason for the existence of this peak in pouch-grooming is not clear, but it may be due to sampling-error. Pouch-grooming was a relatively infrequent event (Table 3.3.20) and there were also large variations in frequencies between female subjects (Figure 3.3.15).

3.4.5 Allogrooming

Allogrooming occurred in several different contexts in captive *T. billardierii*, which are discussed in Section 2.3. There was no significant difference in the frequency of allogrooming between hours of the day, due in part to the overall low frequency of its occurrence and also

to its relationship to the various other types of behaviour. It was recorded in only M1, F1 and F6 in this phase of the study. Allogrooming by M1 was directed principally toward F1 whilst they were resting together. Allogrooming by F1 and F6 was mainly directed toward each other, although a small portion of the scores of F1 consisted of acts of grooming M1. Allogrooming is discussed in relation to sexual interactions (Chapter 4), agonistic interactions (Chapter 5) and mother-offspring relations (Chapter 6).

3.4.6 Sexual Interactions and Non-sexual Interactions

There were no differences in the frequency of sexual interactions between males or between hours of the day (Table 3.3.12) but this was presumably largely due to the small size of observational samples and low observed frequencies of these interactions. Both sexual interactions and other types of interactions occurring between subjects were observed to be most frequent in the few hours following sunset and a comparable period preceding dawn (Figures 3.3.11 and 3.3.12).

Differences between the frequency of non-sexual interactions between subjects and hours of the day were revealed in the analysis of the data, but no significant differences occurred between individual subjects (Table 3.3.15).

Both sexual interactions and agonistic interactions are discussed in greater detail in subsequent sections (Chapters 4 and 5).

CHAPTER 4

SEXUAL INTERACTIONS

4.1 INTRODUCTION

Sexual behaviour consists of elements of behaviour that are concerned with ensuring contact between individuals of opposite sex for the purpose of mating, i.e. to ensure fertilization (Leuthold 1977).

In studies of macropods, investigations of courtship and mating have generally been purely qualitative. Descriptions of sexual behaviour in *Thylogale billardierii* have been presented by Morton and Burton (1973) and McCartney (1978) but no quantitative study has hitherto been presented. Selected aspects of sexual behaviour have been treated quantitatively in *Macropus rufus* (Croft 1981a), *M. robustus* (Croft 1981b) and *M. parryi* (Kaufmann 1974a).

In view of this paucity of information available on the sexual behaviour of macropods a part of the study was devoted to investigate sexual interactions in *T. billardierii*.

4.2 ANOESTROUS COURTSHIP

4.2.1 Methods

During the study of diel activity-patterns (Section 3.2) any interactions between subjects that were observed were recorded, in the interval between the obtaining of scan-samples. However, continuous gathering of scan-samples prevented the compilation of exhaustive records. Subsequent to the study of activity-patterns, observations were, therefore, undertaken with the aim of assembling more accurate and complete chronicles of sexual behaviour and agonistic behaviour (Chapter 5).

A total of twenty-five 2 hour observation sessions were amassed over a seven week period (5.8.1982 to 24.9.1982). A cassette-recorder was used to record verbal accounts of all sexual and agonistic interactions observed, as they occurred. The recorded descriptions so obtained were transcribed on standard protocol sheets at a later date. Only records

of sexual interactions gathered by this method were considered in detailed analyses of behavioural events.

Conditions of the study were as described in Section 3.2, except that observations were performed from a 1.5 m x 1.5 m x 1.8 m room situated where the original observation hide was previously positioned (Figure 2.1).

An additional male subject (M2) was also introduced to the compound at the commencement of this stage of the study and a female subject (F2) was introduced later during the course of this study.

Analyses of sequences of behavioural events occurring during anoestrous rous courting were performed according to the method described by Chatfield and Lemon (1970) using a χ^2 "goodness-of-fit" test. Behavioural events identified for analysis are presented in Table 4.1, and are described qualitatively in Section 4.2.2. Due to the essential passivity of female subjects during sexual encounters, only two sets of first order transitions of behavioural events were analysed in detail *viz*. Male→Male and Male→Female.

All behavioural events identified for analysis were based on active processes and all of them could therefore be preceded and followed by more passive forms of behaviour i.e. standing. Passive behavioural events were omitted for three reasons - since the behaviours of two individuals were recorded simultaneously, the cataloguing of all body-postures during an interaction was not feasible; such events were usually brief transitional states between the behavioural events actually used. Furthermore, by omitting passive behavioural events the categories used in analysis could be treated as discrete and as such, could easily be tested for independence.

According to the broad criteria employed in the analysis, any behavioural event may theoretically follow one of the same category or any other event. Slater and Ollason (1972) recommended eliminating homogeneous transitions from analysis as there is often a tendency for

TABLE 4.1 Inventory of behavioural events identified in anoestrous courting with their respective symbols.

Approach	AP
Leave	LE
Nose-sniffing	NS
Pouch investigation	PI
Genital investigation	GI
Coquet	CO
Holding	HO
Flank grasping	FG
Cuffing	CF
Other	OT
Allogrooming	
Autogrooming	
Standing full stretch	
Turning	
Feeding	
Biting	

behavioural events to occur in bouts; consequently, the inclusion of these transitions may obscure more interesting relationships between behaviours. However, in the present study homogeneous transitions were rare and were included for convenience of analysis. The calculation of expected values for truncated contingency tables cannot be performed in the manner applied to complete tables, i.e. (row total x column total) ÷grand total (Slater and Ollason *op. cit.*). Expected values must be calculated so that zero values are listed at all points of the matrix where observed values cannot occur for either of the two reasons stated above. Goodmann (1968) presented a method for the analysis of "quasi-independence" in truncated contingency tables which fulfils these criteria, however it is very complicated because the expected values can only be calculated by a process of iteration (Slater and Ollason *op. cit.*).

4.2.2 Inventory and Qualitative Description of Behavioural Events

(a) Approach

In the majority of recorded instances, the male initiated sexual interactions (Section 4.3). The method of locomotion employed by males, for approaching females was typically slow progression (Section 2.3) or, occasionally, slow bipedal hopping. Male individuals were sometimes heard to utter the "clucking" vocalization (Chapter 7) while approaching a female, however, from the observer's position this could not always be detected and therefore, its frequency of occurrence could not be precisely ascertained. M1 apparently vocalized in this manner with greater regularity in this context than either M2 or M3.

(b) Nose-Sniffing

This behavioural event is described in Section 2.3 (Plate 2.3.5). It was of a very common occurrence preceding sexual interactions and was generally performed by males; however, it was sometimes also noted in

female subjects.

(c) Genital Investigation

Male subjects frequently placed their nose near the urogenital opening of females. During genital investigation, the male typically positioned its head either beneath the female's tail and behind her hind legs (Plate 4.2.1) or, less frequently, under her abdomen and in front of her hind legs. After performing this action, the male usually adopted an upright position and was occasionally observed to lick its lips. No overt flehmen (lip-retraction and/or baring of teeth) behaviour was observed. On two separate occasions, one female subject was observed to urinate during genital investigation, the male inserted its nose into the stream of urine and then engaged in licking its lips.

(d) Pouch Investigation

Males were often observed to attempt sniffing at the pouch-area of a female subject (Plate 4.2.2). Occasionally, the male used its fore-paw(s) to open the pouch aperture and then inserted its nose in the pouch. For the purposes of analysis, all episodes involving the orientation of the male's head towards the region of the female's pouch which may have resulted in contact between the two individuals, were scored as pertaining to this category of behaviour.

(e) Coquet

This behavioural event was previously termed courting by Morton and Burton (1973); however, as courting is commonly used to designate a complete, complex and often heterogeneously motivated series of sexual interactions, in an attempt to avoid possible ambiguity, the present author selected this term. In coquet behaviour the male generally stands erect (Section 2.3) in front of the female thereafter alternately pushing and pulling her gently until she assumed an upright posture (Plate 4.2.3).

PLATE 4.2.1: Genital investigation

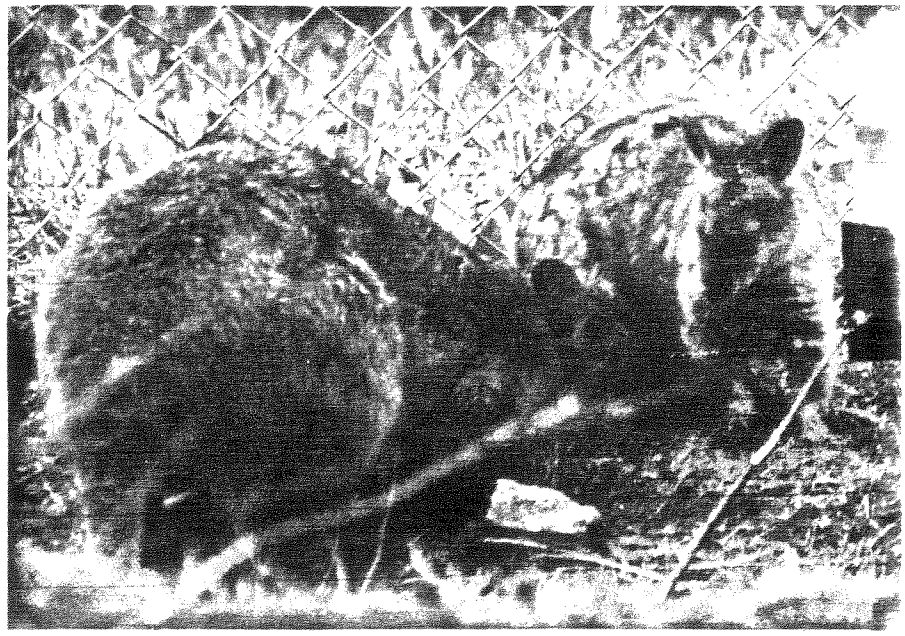


PLATE 4.2.2: Pouch investigation

PLATE 4.2.3: Coquet

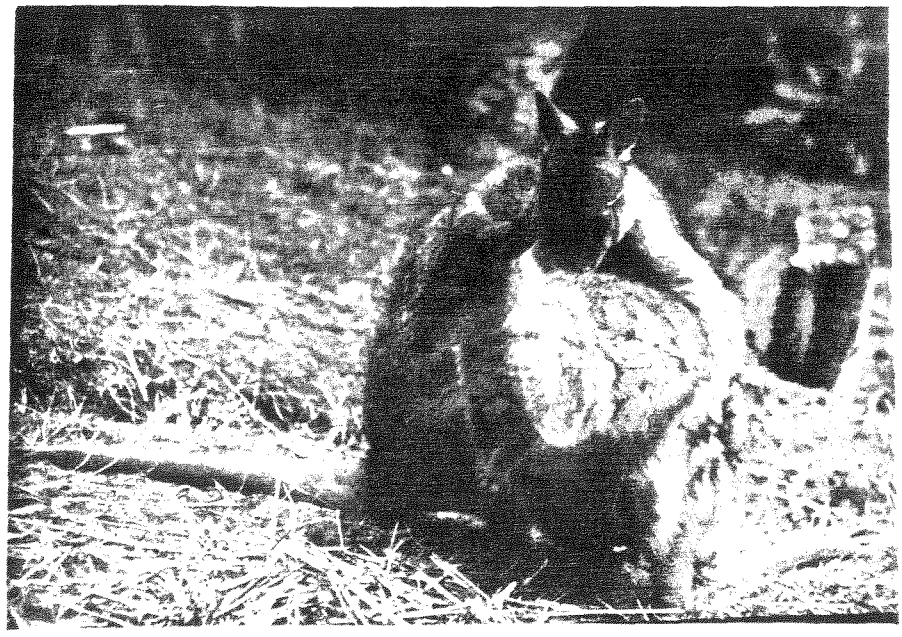


PLATE 4.2.4: Flank grasping

The male then often continued pulling her and pawing her about the head and shoulders. During this process, the male was frequently observed to toss its head completely backwards, exposing its throat.

(f) Holding

After coquet, the male often held the female in an upright position for varying periods of time. Occasionally, the female reciprocated this and both animals thus assumed a position similar to that employed in grappling, noted in the context of male-male interactions (Section 5.3, Figure 5.3.2), however both animals kept their feet flat on the ground in this case. Tossing the head backwards by males also occurred on a few occasions during this event.

(g) Flank Grasping

After any of the above behaviours, a male sometimes moved to the rear of the female and grasped her around the flanks (Plate 4.2.4). The female then usually moved away. The male thereupon generally reapproached the female clasping her around the flanks and this sequence was often repeated several times.

(h) Cuffing

This term is largely self explanatory. Both males and females were observed to cuff their consorts during sexual encounters. Cuffing by males was usually associated with coquet behaviour.

(i) Erection of the Penis

The males' penis were occasionally observed to be in a state of erection during the course of sexual interactions. M3 erected its penis more frequently in this context than either M1 or M2. The penis was often everted from its sheath without being fully erected. Licking of the penis to promote erection was rare.

(j) Pelvic Thrusting

Pelvic thrusting by males, when not in contact with a female subject was observed only twice (once in M1 and once in M3) and never in one of the planned observation-sessions. Similar behaviour was observed in captive male *T. billardierii* by Morton and Burton (*op. cit.*).

(k) Allogrooming

Both males and females were observed to groom their consort during the course of sexual interactions. As with allogrooming occurring in other contexts, it was directed toward the head and/or neck of the recipient. Females were occasionally observed to severely bite males during sexual interactions. This was apparently an agonistic action whereas normal allogrooming appeared, in all respects, amicable in nature.

(l) Leaving

In the majority of episodes of courting, sexual interactions were terminated by females (Section 4.3). Generally, their method of locomotion when leaving was either slow progression, or slow bipedal hopping, although occasionally when a male was particularly zealous in his attentions, the females decamped more rapidly.

4.2.3 Analysis of Behavioural Events Occurring in Anoestrous Courtship

A diagrammatic representation of the results of analyses of the sequences of events recorded in anoestrous courtship is presented in Figure 4.2.1. The diagram was constructed by combining the results of the two sets of transition analyses (male-male, male-female) used in the study. Table 4.2.1 shows the results of the χ^2 tests of each of the contingency tables generated in these analyses.

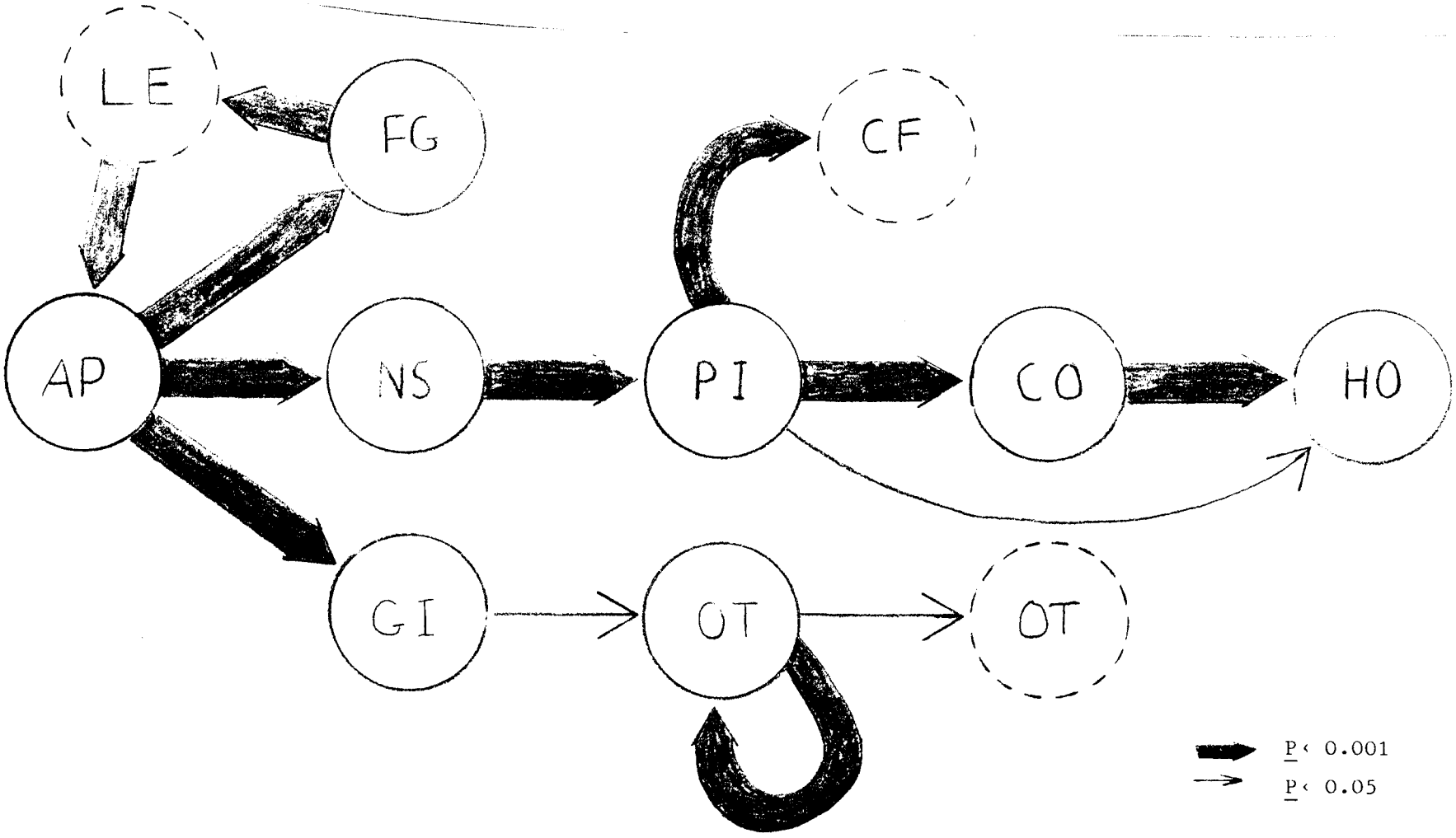


FIGURE 4.2.1: Summary of the results of transaction flow analyses of events occurring in anoestrous courtship. Solid circles = male events, dashed circles = female events. Symbols defined in Table 4.1.

TABLE 4.2.1 χ^2 values of the two transition analyses of behavioural events observed during anoestrous courtship.

First order transition	χ^2 value	P.	Number of fe <1	Percentage of fe <5
Male → Male	531.08	<0.001	0	14
Male → Female	56.38	<0.001	0	22

In accordance with Cochran's (1954) recommendations that none of the expected values of the contingency table should be less than one and not more than twenty percent of any value less than five, infrequent behavioural events were combined into the "other" category (Table 4.1) to ensure that these conditions were fulfilled. This involved condensation of the original 14 x 14 male-male contingency table to an 8 x 8 table and the original 14 x 12 male-female contingency table to a 3 x 3 table. Although in the latter scheme 22% of the expected values were less than five, it is believed that this fact does not invalidate the analysis, given the very low probability (<0.001) of random associations between the constituent behavioural events. The observed frequencies of female-male and female-female transitions of behavioural events were too low to fulfil the requirements stipulated for this analysis, and this result is in agreement with the observation that female subjects are essentially passive during sexual interactions.

The frequencies of the various behavioural events observed in sexual interactions are shown in Table 4.2.2.

4.2.4 The Frequencies and Durations of Anoestrous Courtship

The recorded frequencies of sexual interactions between male and female subjects are shown in Table 4.2.3. Data for M1 and M3 includes recorded instances of sexual interactions obtained during the phase of the study devoted to the investigation of diel activity patterns (Section 4.2.1). The results obtained for these individuals during a comparable

TABLE 4.2.2 Frequencies of various behavioural events for male and female *Thylogale billardierii* recorded during sexual interactions (N = 94).

Behavioural Event	Male s.s.	Female s.s.
Approach	2.02	0.14
Leave	0.34	1.83
Nose-sniffing	0.51	0.07
Pouch investigation	0.66	-
Genital investigation	0.89	-
Coquet	0.90	-
Holding	0.69	0.09
Autogrooming	0.08	0.02
Allogrooming	0.10	0.05
Cuffing	0.04	0.27
Standing full-stretch	0.04	-
Flank grasping	0.74	-
Biting	-	0.03

TABLE 4.2.3 Frequencies of sexual interactions in captive *T. billardierii* (see text for elucidation).

Male \ Female	F1	F3	F4	F5	F6	F2*	Total
M1	21	0	1	13	26	4	65 (31)
M3	5	13	35	7	4	3	67 (30)
M2	5	2	1	19	5	2	34
TOTAL	31	15	37	39	35	9	166

* Data pertaining to F2 is based only on 16 hours of planned observation-sessions.

number of sampling sessions as that used to study the behaviour of M2 is indicated in parenthesis.

The mean durations of sexual interactions are presented in Table 4.2.4. Only interactions that exceeded 5 seconds in duration and less than 5 minutes were treated in this analysis. Brief encounters between males and females were usually not overtly sexual in nature; the majority of such interactions were either agonistic (Section 5.2) or consisted of brief nose-sniffing, not followed by further interaction between the two subjects. During the course of prolonged sexual interactions, subjects typically moved out of the visual field of the observer, consequently it could not be ascertained when a particular interaction terminated and a subsequent one commenced.

TABLE 4.2.4 Mean durations (seconds) of dyadic sexual interactions between individual pairs of male-female subjects.

Females s.s. / Males s.s.	F1	F2*	F3	F4	F5	F6
M1 mean	28.4	34.0	-	-	36.75	52.53
s.d.	15.79	41.69	-	-	29.93	38.81
n	5	4	-	-	8	15
M2 mean	15.67	5.00	-	-	47.67	33.75
s.d.	6.02	1.41	-	-	34.84	24.96
n	3	2	-	-	15	4
M3 mean	52.5	47.33	12.5	86.92	20	34.00
s.d.	37.75	30.44	3.54	42.45	0	15.41
n	4	3	2	13	1	4
Total mean	33.25	32.00	12.5	86.92	42.88	46.04
s.d.	26.75	34.00	3.54	42.45	32.59	34.03
n	12	9	2	13	24	23

* Data pertaining to F2 is based on only 16 hours of systematic observations.

4.2.5 Discussion

The behaviour of *Thylogale billardierii* during anoestrous courtship is similar in many respects to that of other species of macropodines so far investigated but differs from the latter in a few respects. A summary of behavioural events occurring in anoestrous courtship in the subfamily Macropodinae is presented in Table 4.2.5.

Sniffing and licking of the urinogenital region is common in all macropodines so far investigated except *Setonix brachyurus*. Urinating by females during this process has been noted in *M. rufus, M. giganteus, M. robustus, M. fuliginosus, M. agilis, M. antilopinus, M. rufogriseus* (Coulson and Croft 1981), *M. parryi* (Kaufmann 1974a) and *T. billardierii* (this study). Johnson (1977a) reported that male *T. thetis* were observed to mouth the ground where females had previously urinated. Male *M. parma* exhibit a similar interest in fresh urine (Maynes 1973). Flehmen behaviour has been reported in *Dendrolagus dorianus* (Ganslosser 1979 after Coulson and Croft *op. cit.*), *M. fuliginosus* (Coulson and Croft *op. cit.*) and in *M. antilopinus*; in the latter species it is apparently more pronounced in expression (Croft 1982).

The "licking of the lips" component exhibited by male *T. billardierii* may indicate that the subjects were attempting to detect specific substances in the urine, possibly assisting them determine the reproductive state of a female. The frequency of genital investigation in male *T. billardierii* (Table 4.2.5) and its almost universal occurrence in all macropodines so far investigated suggests that it may have an important function in enabling males to detect oestrous in females.

Pouch-investigation, by contrast, is apparently uncommon in the larger macropods *M. rufus* and *M. robustus* (Croft 1981a, b). Opening of the pouch of a female with the forepaws and inserting the nose has only been noted in *T. thetis* (Johnson 1977a) and in *T. billardierii* (McCartney 1978, and this study). Pouch-investigation may occur for one of several

TABLE 4.2.5 Summary of various behavioural events occurring in anoestrous courtship in the subfamily Macropodinae. (+) recorded, (-) not recorded, (±) rare, (?) uncertain. Actual percentages of the number of sexual encounters in which behavioural events occurred are indicated where known.
N.B. not recorded does not necessarily mean that the event does not occur.
* Observed in captive individuals by Sharman *et al.* (1966).
† Similar to *T. billardierii* but not identical.
Modified in part from Croft 1982.

Species	Behaviour Pattern: Genital-Investigation	Pouch-Investigation	Displaying Ventral Surface	Flank-Grasping	Tail Grasping	Sternal Rubbing	Coquet	Allo-Grooming	Captive (c) or free living(f)	Source
Macropus rufus	68-87.4%	10.5-20*	-	-	18.4-24†	-	-	-	f	Croft 1981a; Russell 1970b
M. robustus erubescens	45-57.3%	0-2.3%	+	-	+	-	-	-	f	Croft 1981b
M. giganteus	+	-*	+	-	+	+	-	+	c,f	Grant 1974; Kaufmann 1975
M. billardierii	+	-	+	-	+	+	-	-	c?	Croft 1982
M. antilopinus	+	-	+	-	-	-	-	-	f	Croft 1982
M. parryi	+	+	+	-	+	Pawing	+?	-	f	Kaufmann 1974a
M. rufogriseus	+	-	-	+	-	-	-	+	c	Lafollette 1971
M. agilis	+	+	+	-?	-	-	+	-	c	Johnson 1977a
M. eugenii	54.4%	9.1%	+	22.7%	-	-	+	+	c	This study
Setonix brachyurus	+	-	+	-	-	-	-	-	c	Packer 1969

reasons. The presence of a very large pouch-young or the absence of pouch-young may provide a premonitory indication to males that a female might come into oestrous shortly (Section 2.2). However, such features can be expected to provide only very general information. Males sexually investigate females regularly. An average frequency of 1.78 sexual interactions/per female/per day was recorded for M1 and M3 over the four day sampling-period during the study of diel activity patterns (Section 3.2). This probably is a very conservative estimate, since not all sexual interactions were scored during this period. The oestrous period in macropods is generally very brief, probably less than one day (Tyndale-Biscoe 1973). It is, therefore, probable that males seek for some more precise cues to indicate whether females are receptive or not. The lining of the pouch changes from its normal dark, scaly appearance immediately before paturation acquiring a pink, clean and moist appearance in *T. billardierii* (Rose *pers. comm.*), similarly to the larger macropods (Tyndale-Biscoe *op. cit.*).

Since paturation is followed by oestrous in *T. billardierii* (McCartney 1978), modification of the lining of the pouch may be an important potential index of impending oestrous to males. If it is these changes in the pouch at paturation that males are seeking, then it may be expected that in macropods where no postpartum oestrous occurs (e.g. *M. giganteus* and *M. fuliginosus*, Tyndale-Biscoe *op. cit.*) that males would show little interest in the pouch region. No studies have so far been undertaken on the frequencies of behavioural events during anoestrous courtship in such Macropods.

Odourous substances secreted by the pouch may also indicate the reproductive state of a female; however, the occurrence and function of such processes have not yet been investigated. Aprocrine glands have been identified in the pouch region of large macropods (Mykytowycz and Nay 1964).

Displaying of the ventral surface to a female is also a common feature of anoestrous courting in macropodines, but the active inducement of females to assume an upright posture and holding of females has only been reported in the genus *Thylogale*. Similar behaviour has been noted in *M. parryi* (Kaufmann 1974a); however in this species it differs in some respects to that exhibited by *T. billardierii;* the male *M. parryi* typically paws and cuffs gently at the female occasionally resting its paws on her shoulder.

The reason for exhibiting the ventral surface by male macropods and for associated behavioural events is not clear. It may be related to the presence of sternal glands in the male. *M. giganteus* actively rub their chests against the heads of females (Grant 1974). The presence of convoluted apocrine glands in the sternal region has been reported in male *M. rufus, M. giganteus, M. robustus* and *Wallabia bicolor* (Mykytowycz and Nay 1964). The possible presence of sternal glands in *T. billardierii* has not been investigated.

The function of precopulatory behaviour is not only important in ascertaining the reproductive state of females by males, but may also serve to satisfy the requisite of males to demonstrate their suitability as prospective mates. It may be to the optimal advantage of females to permit only the "fittest" male to copulate with her and to ensure thereby that her own substantial reproductive investment is not wasted. It is a common attribute of male ungulates to have elaborate weapons used for intraspecific fighting; horns, antlers and tusks probably have some signal function in male bovids and females may recognize these as diagnostic of suitable and competent mates (Walther 1974).

Sexual dimorphism with respect to weight has been noted in many macropods. Johnson (1977a) found that in *T. thetis* the difference in weight between the sexes is mainly attributable to the larger forelimbs and chest regions of males. Male *T. billardierii* also have more robust thoracic musculature and larger forelimbs than females (Rose and Johnson

in press, pers. obs., *vide* frontispiece).

The occurrence of dimorphism is apparently important in male-male interactions. Dominance in such encounters may be related to mating success in *T. billardierii* (Section 4.4) and it has been noted that dominant individuals monopolise oestrous females in *M. rufus* (Croft 1981a), *M. robustus erubescens* (Croft 1981b) and *M. parryi* (Kaufmann 1974a). It is therefore tentatively hypothesised that the coquet behaviour observed in male *T. billardierii* has some general signal function, indicating to the female the potential suitability as a mating partner of her wooer.

It may be expected that males induced females to assume an upright position in order to facilitate examination of the pouch and/or cloacal region. However, the results of transaction-flow analyses (Figure 4.2.1) indicate that coquet followed, rather than preceded, both of these behavioural events.

Both pouch investigation and flank-grasping appeared to occasion some annoyance for females. Pouch-investigation was followed significantly more often than expected by females cuffing males and all instances of females biting males were also observed in this context. Flank-grasping by males almost invariably induced leaving by anoestrous females. It may be further expected that anoestrous females would avoid mating as it is unlikely to be of any benefit to them and may even cause physical damage.

There was a notable difference in the sexual following behaviour of *T. billardierii* and the corresponding event observed in larger macropods. Male *T. billardierii* approached females from the rear and attempted to grasp them in the region of the flanks, whereas in all larger macropods, males grasp females by the tails, usually either at the distal end or the base. Similar vocalizations to the "clucking" noises uttered by male *T. billardierii* at such times have been noted in most macropodines (Section 7.4).

Although bouts of allogrooming did occur, they were relatively infrequent in the context of anoestrous courtship in *T. billardierii*. Behaviours such as this are often amplified in frequency in captivity (Leuthold 1977). Allogrooming may play a role in social facilitation during sexual interactions and is also of frequent occurrence in another common type of male-female interaction, the behaviour termed "resting together" (Section 2.3). Such grooming has also been reported to occur during sexual interactions of free-living *M. rufogriseus* (Kaufmann 1974a), captive *M. rufogriseus frutica* (Lafollette 1971) and for *S. brachyurus* (Kitchener 1970 after Kaufmann 1974a).

The results of the transaction-flow analyses yielded consistent trends of good predictability of the sequence of events occurring in anoestrous courtship (Figure 4.2.1). A few points need to be made in relation to this. The large number of "Male approaches → flank grasps female → female leaves" sequences obscure the fact that females often moved away during any stage of the courtship interaction. Males did not attempt to grasp the flanks of females after the initial approach during a sexual interaction. A combination of the other behavioural events invariably occurred before often recurring sequence: approach-flank grasp cycle commenced.

It was not possible to perform quantitative analyses of any changes in the sequences of behaviour occurring in anoestrous courtship as females approached oestrous. There were a few general trends with respect to the durations of the periods that males spent interacting with each female (Table 4.2.4). During this section of the study F4 and F6 had no pouch young and F5 carried an advanced pouch young (19-26 weeks), consequently each of these subjects had a higher probability of coming into oestrous than F1 and F3 who had mid-term pouch young (7-20 weeks). Generally, males spent more time investigating and following the former group of females than the latter; however, because of the small size of samples, no reliable conclusions can be drawn. It was noted that two days before

F5 came into oestrous M2 spent almost all of a 2h observation-session following it and grasping its flanks (this episode was not included in any of the analyses of either sequences of behavioural events or durations of sexual interactions in order to exclude possible bias). Increased values of the frequencies and durations of sexual interactions as females approached oestrous have been recorded in *M. rufus* (Sharman and Calaby 1964), *M. robustus erubescens* (Croft 1981b), *M. parryi* (Kaufmann 1974a) and *M. parma* (Maynes 1973).

Males did not distribute their attentions equally among females (Table 4.2.3). For example, M3 interacted with F4 in 94.6 per cent of the observed interactions of F4, and M1 interacted with F1 in 67.7 per cent of the sexual interactions recorded for F1. The reason for this is not clear. Males genuinely appeared to prefer the company of particular females, and this predilection did not appear to be related in any way to the reproductive state of the females. F3 was not observed to interact at high frequencies with the males present in the enclosure at any stage during the course of the year even when she had no pouch young. M1 associated with F1 and F5 very frequently throughout the whole study-period, commonly resting with each of them. Its preference for resting-companions alternated between these females over the course of the year. M2 was observed, on a few occasions, to rest with F2, after the completion of this phase of the study (M1 was not present in the enclosure at this stage; it had previously died on 2.10.1982 v. Appendix 2). M2 and F2 had been present together in the upper compound for most of the year. M2 or M3 were never observed to rest with any female during the course of the study. A similar apparent preference by males for certain females is exhibited by captive *Bettongia lesueuri* (Stodart 1966). Stable bonds between males and females are common in *S. brachyrus* (Kitchener 1972) and *Petrogale puella* (Davies 1979).

No quantitative investigation has yet been undertaken on the group-structure of free-living *T. billardierii*. Rose and Johnson (in press)

state that there is no evidence of any persistent social bonds between individuals. From the results of the present study, it is clear that *T. billardierii* have the capacity for individual recognition probably based, at least partly, on olfactory cues obtained by nose-sniffing (Section 2.3).

4.3 THE ROLE OF MALES AND FEMALES IN THE MAINTENANCE OF SPATIAL PROXIMITY

4.3.1 Methods

For the purpose of assessing the role of each sex in the maintenance of mutual proximity, the following events were recorded:

1. Approaches of individuals of one sex towards a quadrat (Figure 2.1) in which an individual (or individuals) of the opposite sex was present (AQ♂ = approach by male; AQ♀ = approach by female).
2. Approaches of individuals to an individual of the opposite sex where bodily contact could, or did, occur (AN♂ = approach by male; AN♀ = approach by female).
3. The leaving of an individual from a quadrat in which individual(s) of the opposite sex were present (LQ♂ = leaving by male, LQ♀ = leaving by female).
4. The departure of an individual from a position next to an individual of the opposite sex, where bodily contact occurred, or could have occurred (LN♂ = leaving by males, LQ♀ = leaving by female).

Movements of individuals in the peripheral regions of the enclosure were not recorded, in order to avoid unrealistic frequencies of approaches and departures due to the fence-running (Section 2.3) activities of certain subjects.

Records of the above events were obtained during ten 2 h observation-

sessions over a two-week period (19.8.1982 to 1.9.1982). Observation-sessions were distributed between the hours of 0400h - 0700 h or 1600h - 1900h, as these were the periods when most active interactions between subjects occurred. Also during this period, similar data were collected for assessing the spatial relationships between F1 and her offspring F6 (Section 6.3).

Analyses of the data were performed following the methods prescribed by Hinde and Atkinson (1970). In the assessment the roles of social partners in maintaining mutual proximity, ideally the following criteria should be attained:

1. The behaviour of both partners should be taken into account.
2. The full contributions of both partners in the maintenance of proximity should be represented.
3. Changes in the absolute and relative levels of locomotory-activity of the two individuals considered should not influence the analysis (Hinde and Atkinson *op. cit.*).

The difference between the percentage of approaches and departures due to each partner is considered by Hinde and Atkinson (*op. cit.*) to best satisfy the requirements specified; however, this function does change to some extent with absolute activity-levels of both partners. In view of this, the data for the current analyses were collected over a relatively short period.

In addition, a χ^2-analysis was performed, comparing the frequencies of the recorded events obtained for each sex (i.e. AQ♂ vs AQ♀, AN♂ vs AN♀ etc.) to determine if there were actual differences between the frequencies of events associated with each sex. As there were unequal numbers of individuals of each sexual category ($n♂ = 3$; $n♀ = 5$), it may be expected that if individuals moved about the enclosure independently of one another, then $AQ♂ = 5/8\ AQ_T$ (where $AQ_T = AQ♂ + AQ♀$) and similarly $AN♂ = 5/8\ AN_T$). However, if individuals moved about at random, then

$LQ\sigma = LQ\varphi$ and $LN\sigma = LN\varphi$ as the frequency of departures is independent of the number of individuals of each sex.

In addition, the present author adapted Hinde and Spencer-Booth's (1968 after Hinde and Atkinson *op. cit.*) original formula

$$\left[\frac{A_i \times 100}{A_i + A_j}\right] - \left[\frac{L_i \times 100}{L_i + L_j}\right]$$

where i,j = two individuals being considered, A = approaches, D = departures) in the following manner: As No.σ : No.φ = 3:5 then it would be expected that Aσ : Aφ = 5:3, and Lσ = Lφ; therefore, $\frac{A\sigma}{5} = \frac{A\varphi}{3}$ so the function is now:

$$\left[\frac{A\sigma}{5} \div \left[\frac{A\sigma}{5} + \frac{A\varphi}{3}\right]\right] \times 100 - \frac{L\sigma}{L\sigma + L\varphi} \times 100.$$

The value of this function will be termed mp in all subsequent discussion.

In accordance with this convention, if male subjects were responsible for maintaining proximity to females, the function will be positive ($mp>0$), if both sexes are responsible for maintaining spatial proximity, the function will equal zero ($mp = 0$) and if females are responsible for maintaining proximity, the function will be negative ($mp<0$).

4.3.2 Results

The observed frequencies of approaches and departures by representatives of each sex with respect to the two spatial relationships specified are presented in Table 4.3.1, together with the results of the χ^2 analyses.

The difference between percentages of approaches by male subjects and the percentages of departures by male subjects (a) into and out of quadrats occupied by female subject(s), $mp = -0.81$, (b) to and from a position immediately adjacent to a female subject, $mp = +35.31$.

Individual subjects did not approach or leave quadrats occupied by subjects of the opposite sex with frequencies greater than those that

TABLE 4.3.1 Observed frequencies of approaches (AQ) and leaving (LQ) into and from a quadrat occupied by an individual of the opposite sex and of approaches (AN) and departures (LN) from a position next to a member of the opposite sex. Expected frequencies shown in parenthesis.

	Males	Females	χ^2	P
AQ	80 (88.75)	62 (53.25)	2.30	n.s.
LQ	64 (72.0)	80 (72.0)	1.78	n.s.
AN	34 (27.5)	10 (16.5)	4.10	<0.05
LN	14 (22.0)	30 (22.0)	5.81	<0.05

would have been expected if subjects were moving at random (Table 4.3.1). Therefore males and females were moving about the enclosure apparently independently of each other. This is also shown by the low (near-zero) value of *mp* for approaches and departures into and from a quadrat. These results may be somewhat misleading in that individuals were observed to have slightly different activity-patterns (Section 3.3.1). If individuals of one sex actively maintained distances greater than the length of a quadrat, this fact would also not be revealed by the analysis.

Males approached females significantly more often that the reverse process occurred, at close distances (Table 4.3.1). Males were therefore responsible for initiating the majority of sexual interactions. Females left the vicinity of males at frequencies significantly greater than males left females (Table 4.3.1) and were thus responsible for terminating sexual interactions in most cases. The high positive value of mp for approaches and departures of males from next to females, indicates that the males rather than the females were primarily responsible for the maintenance of very close proximity. In other words, males approached and left females with greater frequency than *vice versa*; consequently the termination of sexual encounters was not entirely the prerogative of females.

4.3.3 Discussion

Croft (1981a,b) found that male *M. rufus* and *M. robustus erubescens* almost invariably initiated sexual interactions and females of these species terminated the majority, but not all, such encounters.

Female *T. billardierii* approached males in 29% (Table 4.3.1) of all of the recorded interactions, therefore they differed in this respect from female *M. rufus* and *M. robustus erubescens* (Croft 1982a,b) which both initiated less than 5% of sexual interactions. As previously mentioned, the effects of captivity may influence interactions between individuals. Field-studies are necessary to elucidate this aspect of the behaviour of *T. billardierii* and to verify these results.

Although few quantified studies have been undertaken on sexual interactions in macropods, the males apparently take the dominant role with respect to the initiation of such encounters. A notable exception to this may be female *Setonix brachyurus* which take a more active role in sexual interactions (Packer 1969).

Male ungulates also play the more active role in sexual interactions (Leuthold 1977).

4.4 MATING BEHAVIOUR

4.4.1 Methods

In addition to systematically planned observation-sessions (Sections 3.2 and 4.2.1) more casual, periodic observations were undertaken during the course of the study with the aim of recording paturation, mating and associated behaviours. Also, on two occasions, two female subjects were injected with bromocriptine (CB154) (v. Appendix 3) at a dosage of 5 mg/kg of body weight. Bromocriptine is known to induce reactivation of dormant blastocysts in lactating female *Macropus eugneii* resulting in birth 26-28 days after administration (Tyndale-Biscoe 1979). The administration of this drug to lactating female *T. billardierii* has

resulted in birth 26-30 days subsequently (Rose *pers. comm.*); however, this did not occur in every case.

Only one complete mating interaction (26.9.1982) was observed. After the study period was completed, a bout of copulation was observed that was already in progress (5.11.1982).

4.4.2 Description of the Events Associated with Mating Behaviour

At the time of the observed bout of copulation, three males were present in the enclosure. F5 was observed licking around its cloaca, when the investigator first entered the enclosure (1240h). All other subjects were resting at this stage. At 1251h, M2 began chasing F5 around the enclosure and this activity continued for 2 min. At one stage, during the pursuit of F5 by M2, M1 and M2 snuffled briefly and subsequently M2 attacked almost every subject present in the enclosure. At 1300h, M2 was placed in the adjacent enclosure. F5 settled down in one corner of the enclosure and again licked around its cloacal region. M1 and M2 interacted frequently through the fence: M1 repeatedly rushed at the fence uttering the "clucking" vocalization and a type of "Hiss-growl" vocalization. M2 retreated at each rush of M1 and simultaneously uttered the "Hiss-growl" vocalization. During this period M2 made continued vigorous lateral movements of its tail. At 1335h the first copulation was observed between M1 and M5, a summary of this and all subsequent attempts at mounting are shown in Table 4.4.1. The time M2 was actually actively pelvic thrusting is also shown along with the period of time after mounting this activity commenced. After the first copulation, M2 was reintroduced into the enclosure. Throughout the course of the afternoon, M2 made repeated attempts to move close to F5, occasionally chasing it for short distances, until M1 drove M2 away. During this period, M2 continued to make vigorous lateral movements of its tail. M3 approached M1 and F5 only infrequently and in such instances,

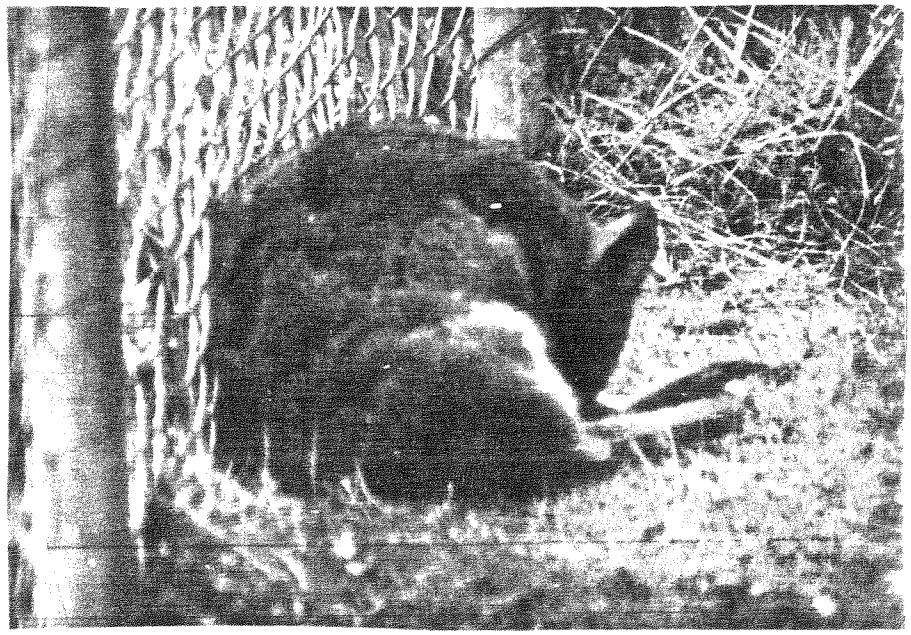


PLATE 4.4.1: F5 licking cloacal region.

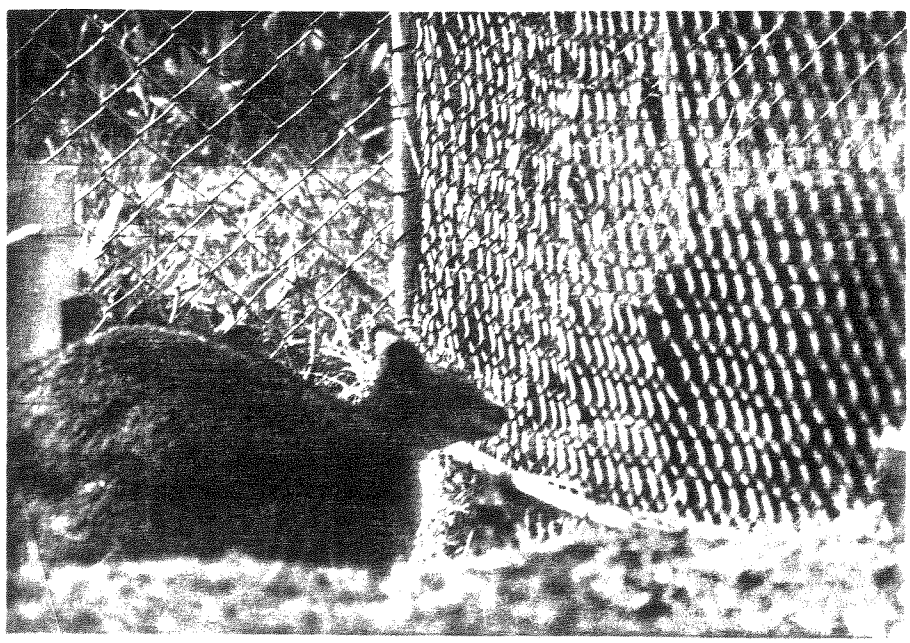


PLATE 4.4.2: M1 (left) and M2 interacting through fence.

PLATE 4.4.3: M1 "coquetting" F5.

PLATE 4.4.4: M1 mounting F5.

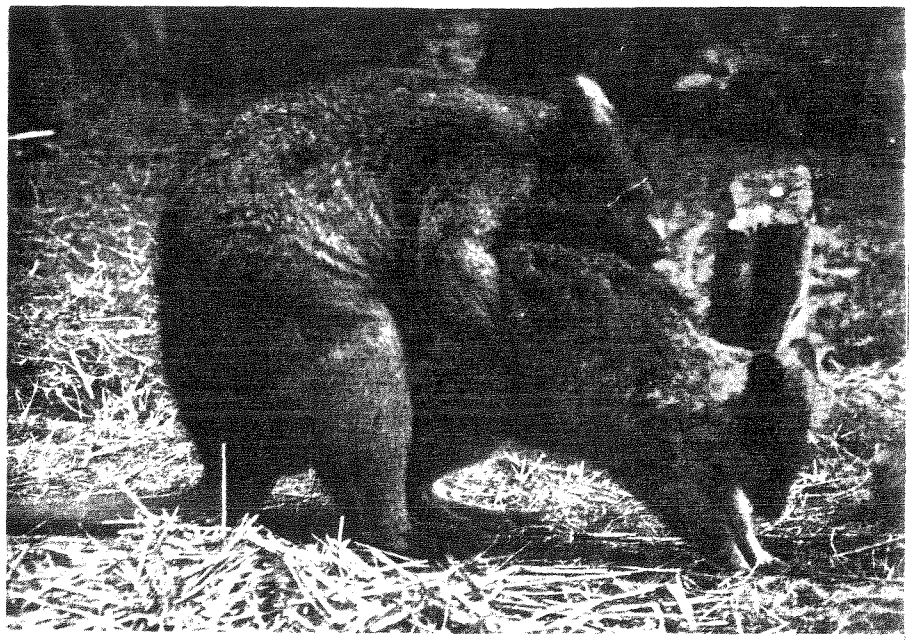


PLATE 4.4.5: Intromission and pelvic thrusting.

PLATE 4.4.6: M1 licking the back of the neck of F5 during copulation.

PLATE 4.4.7: M3 approaching M1 and F5 after the latter pair had ceased copulating.

PLATE 4.4.8: M1 and F5 resting together after a bout of copulation; n.b. the different positons of the animals in comparison with the usual resting together arrangement (v. Plate 2.3.6)

TABLE 4.4.1 Summary of observed attempts at mounting of F5 by M1 (see text for description).

Time	Intromission	Time Mounted	Time Pelvic Thrusting	Reason for Termination
1335h	√	2 min 30 sec	after 50 sec for 1 min 30 sec	M1 released F5
1339h	-	40 sec	-	M1 released F5
1343h	√	3 min 50 sec	intermittently	F5 moved away
1613h	-	5 sec	-	M1 released F5; and drove away M2
1622h	√	1 min 10 sec	after 55 sec for 15 sec	"
1650h	-	1 min 3 sec	-	F5 moved away
1701h	√	4 min 10 sec	After 5 sec for 1 min	"

M1 uttered the "clucking" vocalization which invariably resulted in retreat by M3.

Before the first copulation, M1 briefly exhibited the coquet behaviour towards F5, then mounted her. Throughout the day M1 periodically sniffed the genital and pouch region of F5, although only one instance of genital investigation was observed *ca*. 5 min prior to the first copulation. While mounting F5, M1 periodically licked the back of its neck. Between successive mounts, M1 never strayed more than 5 m from F5, often resting with her. Mutual allogrooming occurred periodically between M1 and F5.

Later in the afternoon (1630h), after M2 had made several attempts to move near F5, it rushed at F5 and gripped it firmly around the flanks for a few seconds until F5 was able to sever contact. M1 chased M2 vigorously for a short time, then M2 started attacking other subjects within the enclosure, so both M2 and M3 were placed in the adjacent enclosure to avoid further disruption.

During the course of a subsequent bout of copulation, a brush-tailed possum *Trichosurus vulpecula,* entered the enclosure and approached M1 and F5. F5 attempted to move away but M1 continued to maintain a firm grip for about 30 sec after which period F5 succeeded in securing her release. The possum then approached closer to M1 and both assumed an upright stance cuffing at each other with their forepaws. M1 then actively attacked the possum. The precise actions employed in the fight were too rapid to discern but M1 apparently bit the possum at some stage of the episode, as it was observed to grip a large tuft of fur in its mouth when the interaction was terminated. After this brief scuffle, both protagonists retreated simultaneously, the possum climbing on the nearest tree. One final copulation was seen after this (2137h). At 0038h (27.9.1982) M1 made repeated efforts to mount F5 but it moved away on each occasion. Observations were terminated at 0130h with M1 still being near to F5.

M1 and F5 were observed to be resting together 1050h-1230h (27.9.1982) and during subsequent spot-checks of the enclosure that day, M1 remained near F5. At 1100h (28.9.1982) M1 was no longer observed to maintain close proximity to F5.

In the other bout of mating observed M2 was in the process of copulating with F2 when the observer entered the enclosure 1300h (5.11.1982). No subsequent attempts at mounting were observed in the next 4h. At this stage, M2 was the only male subject present in the enclosure. Mutual allogrooming was again observed between the consorts during the course of the afternoon.

4.4.3 Discussion

The copulatory behaviour described above are similar to that described by Morton and Burton (1973) and McCartney (1978) in this species. However, in none of the observed attempts at mounting by M1 of F5 was any "vigorous massaging of the flanks" by the male observed, an event

which each of the former authors described and which has also been noted in *Thylogale thetis* (Johnson 1977a). M2 rubbed the flanks of F2 briefly before dismounting.

The presence of other males had an obvious disrupting effect on mating behaviour. M1 was the dominant male and it is unlikely that even if M2 and M3 were present in the enclosure during the entire period when F5 was in oestrous, either of them would have mated with it. The largest male present apparently enjoyed the exclusive right to mate with an oestrous female in all recorded instances of copulation in *M. rufus* (Croft 1981a), *M. robustus erubescens* (Croft 1981b) and *M. parryi* (Kaufmann 1974a). Mollison (unpub. after McCartney *op. cit.*) stated that female *T. billardierii* were promiscuous. All of the males in this study were clearly different in size (v. Appendix 1); males whose sizes were more closely matched may all have been able to achieve access to an oestrous female.

Captive male *T. billardierii* engaged in regular ritualized encounters (Section 5.3) whose function appeared to maintain a dominance-hierarchy. All interactions during the period when F5 was in oestrous were of a non-ritualized type; in most cases M1 needed only to vocalize and move toward a subordinate male to induce it to retreat. If such dominance-hierarchies occur in free-living *T. billardierii*, it may be expected that alpha males would monopolize oestrous females.

The interspecific agonistic interaction between M1 and the intruding possum may have been atypical but it did appear to indicate the high state of general arousal experienced by M1 during the sexual encounter. In all previously noted interactions between possums and captive *T. billardierii* the pademelons were invariably displaced by the possums. One other such incident, involving M1 and another brush-tailed possum occurred on 9.6.1982 when M1 apparently charged at a possum that was feeding at the food hopper within the enclosure, causing it to retreat by ascending the nearest tree. Free-ranging *T. billardierii* and *Tr. vulpecula* have been observed to share

common nocturnal feeding areas (Johnson 1977b, 1978) but the occurrence of interspecific interactions has not been recorded in such cases.

Vigorous, sinuous lateral movements of the tail has been reported in the smaller macropodids *M.*[*] *rufogriseus*, *M.*[*] *agilis* and *M.*[*] *parryi* (Sharman *et al.* 1966) while they were in the process of examining females. Johnson (1977a) described similar behaviour in male *T. thetis* denied access to an oestrous female, and this phenomenon appears, therefore, to be analagous to the behaviour exhibited by M2 in this study. Kaufmann (1974a) suggests that the tail-lashing behaviour frequently observed in *M. parryi* is a general indication of excitation.

The precise expressions of the behaviour of *T. billardierii* are similar, in most respects, to those described in other small and medium-size macropodines (Sharman *et al.* 1966). There was a large variation in the durations of attempted mounts and the amount of pelvic thrusting. Within the family Macropodidae durations of intromission range from periods as brief as 10 sec in some bouts of mating in *M. parryi* (Kaufmann 1974a) to 53 min in captive grey kangaroos[†] (Poole and Pitton 1964). However, *M. parryi* is characterised by having multiple intromissions within a single bout of copulation and the rapidity of such intromissions was probably due to the disturbing influence of other males (Kaufmann 1974a).

The observed attempts at allogrooming by male *T. billardierii* during mounting of females and reciprocal allogrooming between consorts resting together between copulations has not been reported in any other species of macropod during oestrous courtship. Male *Wallabia bicolor* occasionally scratch vigorously at the backs of females during pre-mating behaviour (Sharman *et al.* 1966).

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[*] Protemnodon

[†] Probably *M. giganteus*

CHAPTER 5

AGONISTIC INTERACTIONS

5.1 INTRODUCTION

Agonistic interactions occurring between individuals have long constituted an area of considerable interest in studies of animal behaviour. However, until recently few detailed investigations have been undertaken on this aspect of the social activities of macropodids and in many instances only anecdotal accounts or information based on cursory observations obtained in the course of some other study have been presented for particular species.

Intraspecific interactions have been documented to some extent in the macropodines *Macropus rufus* (Frith and Calaby 1969; Russell 1970a,b; Croft 1981a), *M. robustus erubescens* (Croft 1981b), *M. giganteus* (Grant 1973, 1974; Kaufmann 1975), *M. antilopinus* (Croft 1982), *M. parryi* (Kaufmann 1974a, *Thylogale brunii* (Ganslosser 1978), *T. thetis* (Johnson 1977a), *T. billardierii* (Morton and Burton 1973) and *Setonix brachyurus* (Packer 1969).

Morton and Burton (1973) found that a near-linear hierarchy existed in captive female *T. billardierii* and the ranks of individuals within the hierarchy was related to their body sizes. The limitations of a zoo study did not allow these authors to investigate some potential aspects of agonistic interactions in this species, such as the effect of the introduction on animals to establish groups and only limited observations were obtained of male-male interactions.

Consequently, the present investigator decided to initiate a study for the purpose of elucidating and expanding what is already known of the agonistic behaviour of *T. billardierii*.

5.2 DOMINANCE-RELATIONSHIPS

5.2.1 Methods

The majority of agonistic interactions observed between captive

T. billardierii were of two types: (a) supplanting of another individual i.e. A approaches B, B moves away. (b) Ritualized fighting (discussed in Section 5.3). It is hypothesized by the author that interactions of type (a) may be expected to provide a good indication of the social structure and organization of the captive subjects.

All active displacements of an individual by another individual that were observed during the section of the study devoted to investigating activity-patterns (Section 3.2) were recorded, as were displacements that were observed during the observation-sessions in which reproductive behaviour was investigated (Section 4.2.1). For the purposes of analysis and discussion, the total period devoted to investigation was subdivided into four parts. Periods 1 and 2 comprised the first and second half of the "activity-patterns" period of study. Period 3 corresponded to the phase of the study when M2 was present in the enclosure, until the beginning of Period 4. Period 4 represents the phase of the study when F2 was introduced into the enclosure.

As the total number of hours of observation and also the times of observation were different in the four periods, the absolute frequencies obtained during each of these are not directly comparable; however, this is not considered to be really important, as it was only the relative frequencies of behaviour yielded by each animal in agonistic interactions that were the principal subject of this investigation.

For the analysis of the data obtained three methods of ranking subjects were used:

(a) actual frequencies of supplanting - if an individual subject supplanted another subject with greater frequency than it was displaced by that subject, then the former individual was adjudged dominant to the second;

(b) success-scores (Russell 1970a) - this value is calculated by dividing the number of successful encounters in which an

individual was involved by the total number of interactions in which it participated;

(c) points-scores (Grant 1973) - calculated on the basis of the success of each individual in its interactions with every other subject. Two points were awarded if an individual was successful (i.e. won encounters) in more than 50% of its interactions with another individual, one point was given to each participant in the case of equal success and none to subjects successful in less than 50% of their encounters with another individual.

In order to estimate the degree of linearity of the observed hierarchies, Landau's (1951 after Bekoff 1977) method was applied to the data. In this technique, the index of linearity, h, is calculated using the following formula:

$$h = \frac{12}{n^3-n} \sum_{a=1}^{n} \left[Va - {}^{(n-1)}/_{2} \right]^2$$

where n = the number of subjects

Va = the number of individuals that an individual (a) dominates.

The term $12/(n^3-n)$ normalizes h, so that values range from 0 to 1. When h=1, the hierarchy is linear and the variance of V_a is at a maximum. When h=0, each subject dominates an equal number of other subjects and Va=0 (after Bekoff *op. cit.*)

5.2.2 Results

The frequencies of observed displacements during the four sample-periods considered are presented in Table 5.2.1, together with the calculated values obtained for h. The ranking of each subject in each of the four sample-periods, based on success-scores (s.s.) and points-scores

TABLE 5.2.1 Frequency of displacement interactions between captive *Thylogale billardierii* and Landau's measure of the degree of linearity of social hierarchies (h) for each observation period.

Period 1		Subordinate						
Displaced		M1	M3	F1	F3	F4	F5	Total
DOMINANT	M1	-	10	0	16	27	0	53
	M3	0	-	0	2	0	26	28
	F1	0	2	-	4	4	6	16
	F3	0	1	0	-	5	4	10
	F4	1	1	0	0	-	4	6
	F5	0	1	0	1	1	-	3
TOTAL		1	15	0	23	37	40	116

h Total = 0.54 h_{σ} = 1 $h_{♀}$ = 1

Period 2		Subordinate						
Displaced		M1	M3	F1	F3	F4	F5	Total
DOMINANT	M1	-	9	0	10	19	1	39
	M3	0	-	0	6	0	30	36
	F1	0	5	-	8	10	9	32
	F3	0	0	0	-	14	9	23
	F4	0	0	0	0	-	13	13
	F5	0	0	0	0	1	-	1
TOTAL		0	14	0	24	44	62	144

h Total = 0.77 h_{σ} = 1 $h_{♀}$ = 1

TABLE 5.2.1 (continued)

Period 3		Subordinate							
Displaced		M1	M2	M3	F1	F3	F4	F5	F6	Total
DOMINANT	M1	-	26	9	1	9	20	1	0	66
	M2	0	-	18	0	13	8	4	2	25
	M3	0	0	-	0	6	3	13	3	45
	F1	0	0	4	-	15	7	10	0	36
	F3	0	0	0	0	-	16	13	11	40
	F4	0	0	0	0	0	-	8	4	12
	F5	0	0	0	0	0	1	-	27	28
	F6	0	1	4	0	3	0	1	-	9
TOTAL		0	27	35	1	46	55	50	47	261

h Total = 0.57 h♂ = 1.00, h♀ = 0.7

Period 4		Subordinate								
Displaced		M1	M2	M3	F1	F2	F3	F4	F5	F6	Total
DOMINANT	M1	-	10	15	0	3	10	7	1	0	46
	M2	0	-	15	0	0	14	11	4	0	44
	M3	0	2	-	0	1	5	1	4	0	13
	F1	0	0	1	-	7	11	7	6	12	44
	F2	0	1	1	0	-	3	2	3	6	16
	F3	0	0	0	0	2	-	12	3	3	20
	F4	0	0	1	0	5	0	-	3	4	13
	F5	0	0	0	0	0	0	0	-	2	2
	F6	0	0	2	0	0	0	0	0	-	2
TOTAL		0	13	35	0	18	43	49	24	27	200

h Total = 0.55 h♂ = 1, h♀ = 0.89

TABLE 5.2.2 Success scores (S.S.), points scores (P.S.) and ranks (R) of individual subjects in a captive group of *Thylogale billardierii* for each observation period.

Period	1				2				
Animal	S.S.	R	P.S.	R	Animal	S.S.	R	P.S.	R
M1	0.98	2	8	2	M1	1.00	=1	9	=1
M3	0.65	3	4	=3	M3	0.72	3	5	3
F1	1.00	1	9	1	F1	1.00	=1	9	=1
F3	0.30	4	4	=3	F3	0.49	4	4	4
F4	0.14	5	4	=3	F4	0.24	5	3	5
F5	0.07	6	1	6	F5	0.02	6	0	6

Period	3				4				
Animal	S.S.	R	P.S.	R	Animal	S.S.	R	P.S.	R
M1	1.00	1	13	1	M1	1.00	=1	14	=1
M2	0.63	3	11	2	M2	0.77	3	10	3
M3	0.42	5	6	=4	M3	0.27	6	6	=6
F1	0.97	2	10	3	F1	1.00	=1	14	=1
F3	0.47	4	6	=4	F2	0.47	4	7	=4
F4	0.18	7	4	=6	F3	0.32	5	6	=5
F5	0.35	6	2	8	F4	0.25	7	7	=4
F6	0.16	8	4	=6	F5	0.08	8	2	9
					F6	0.07	9	4	8

(p.s.), are presented in Table 5.2.2. A diagrammatic representation of the distribution of dominance-hierarchies based on the actual frequencies of supplanting is shown in Figure 5.2.1.

Scores obtained for F6 are not included in Periods 1 and 2, but are discussed in Section 6.2.

The calculated ranks of individuals, based on both success-scores and points-scores, are in close agreement with each other, for all of the sample-periods examined (Table 5.2.2). However, the calculated values of h (Table 5.2.1) suggest that such a scheme of rank-order may not provide completely realistic satisfactory representation of the existing social relationships. As values of h equalling or exceeding 0.9 are generally considered to be an indication of a strong linear hierarchy, whereas values lower than 0.9 indicates a non-linear hierarchy, (Bekoff 1977), when all of the subjects are considered together, the social hierarchy appeared to be non-linear, however when the sexes are considered separately there was, in the majority of instances, an indication of strong linearity.

Exceptions to the above inference is provided in Period 3, when F1 and its offspring F6 did not interact agonistically (Figure 5.2.1) and in Period 4, when F2, F3 and F4 formed an intransitive triad (after Bekoff *op. cit.*).

One consideration that needs to be taken into account is that in a few cases the difference between a dominant and subordinate individual was only on a single observed displacement (e.g. F4 over M3 in Period 1); hence, expressing hierarchies in terms of either absolute frequencies of supplanting or the points-scores method may lead to incorrect assumptions about some relationships. The dominance of M1 over F1 in Period 3 (Figure 5.2.1, Table 5.2.2) probably represents an example of this.

Two clear indications of abrupt changes in dominance-relationships occurred in the course of the study. Between Periods 1 and 2, M3 ceased from being displaced by F3-5), as suggested by

FIGURE 5.2.1 Dominance hierarchies in captive subjects of *Thylogale billardierii* for the four sample-periods. Arrow means "dominant over".

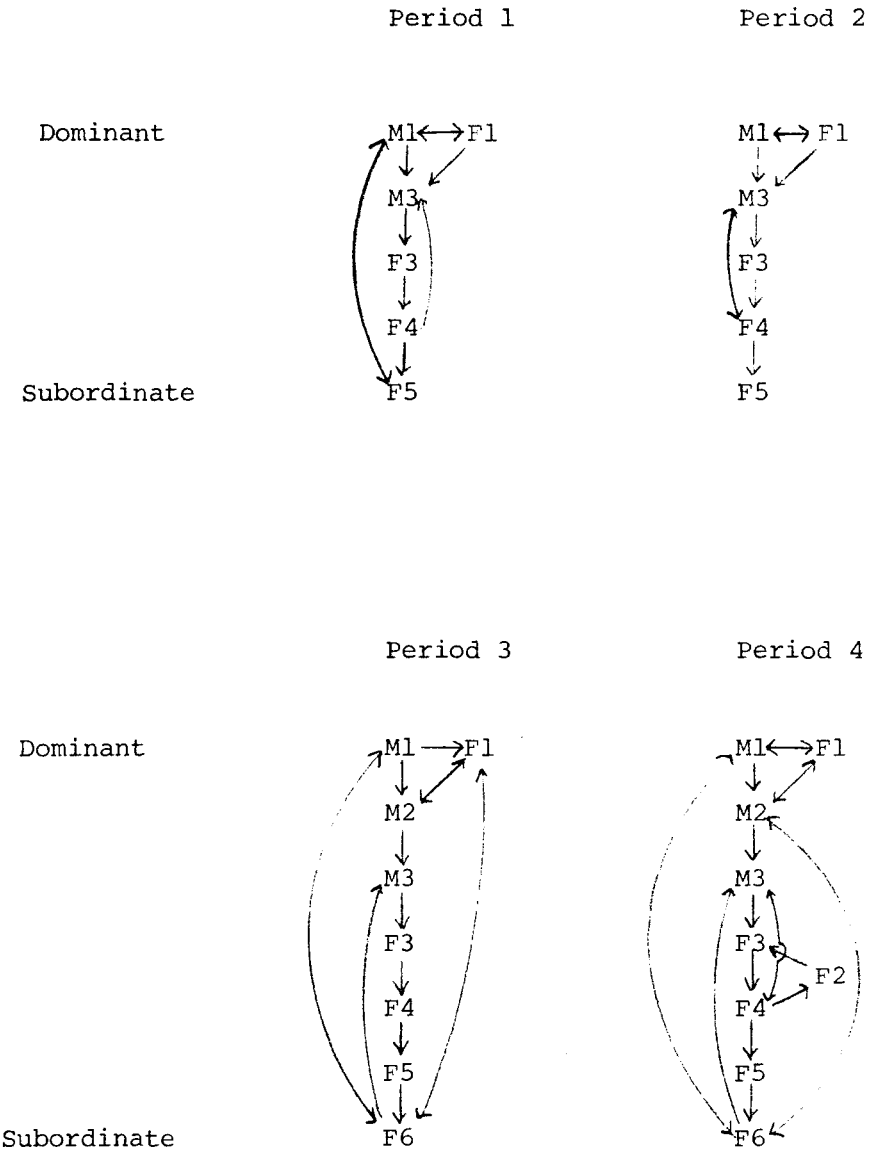


Table 5.2.1, Figure 5.2.1. M3 was sexually immature at the commencement of this study but matured subsequently (v. Appendix 1).

During Period 4, F1 commenced to displace her offspring, F6, actively. This is discussed in more detail in Section 6.3.

M3 supplanted F5 with very high frequencies in both Periods 1 and 2 (Table 5.2.1). Instances of males and females engaging in fights were observed between these two individuals, on three occasions before this phase of the study commenced (5.4.1982, 6.4.1982, 14.5.1982), between M3 and F1 on one occasion (6.4.1982) and between M3 and F6 in numerous instances during Periods 2, 3 and 4 of this study. Fighting in these cases consisted of the acts described by Morton and Burton (1973) *viz.* mutual cuffing and wrestling with the forepaws. M3 emerged as the winner of all fights with F5, usually chasing the latter individual for short periods of time after each interaction. F1 was the apparent winner in the single observed fight against M3. Fights between M3 and F6 were more varied with respect to their outcome but in all observed interactions, M3 retreated more frequently than F6.

M1 supplanted F4 with relatively high frequencies throughout the study. Furthermore, M1 was observed to interact sexually with F4 only once (Section 4.2.4). No overt aggressive interactions were ever observed between these two individuals. The reason for avoidance of approaches of M1 by F4 was not clearly apparent and whether M1 approached with the intent of interacting with it sexually or agonistically could not be determined.

When first introduced to the enclosure, M2 assumed a position in the hierarchy intermediate between M1 and M3. At the beginning of the year M2 was slightly heavier than M1; however, at the time of its introduction it was much lighter (v. Appendix 1).

The position of F2 in the dominance-hierarchy indicates that social rank, at least in the case of females, is not determined solely on the basis of bodyweight. At the time of its introduction, F2 weighed more

than any other female present in the enclosure (v. Appendix 1); however, she was subordinate to both F1 and F4. F1 was considerably heavier at the beginning of the year but had also lost weight subsequently, possibly as a result of rearing two offspring. F4 was 0.5 kg lighter than F2 and also appeared much less robust with respect to its body-construction. Limitations of time prevented continuation of this study, although it would have been interesting to determine if the position of F2 in the hierarchy may have changed with time.

Overt aggressive interactions between females were rare. The day after F2 was introduced, F1 actively attacked it, grabbing it around the flanks and chasing it for a short distance. The other acts of clear aggression observed by females towards other females were mainly directed at F6 by F5 (on numerous occasions), F2 (once) and F1 (Section 6.3). F5 appeared to evidence a particularly high level of intolerance for F6. This may have been related to the fact that F5 carried pouch young of her own at this stage. On two occasions, F6 approached F5 and apparently attempted to place its head near the pouch of the latter, possibly trying to suckle.

At the completion of the study F3 weighed more than F1, but was never observed to displace it.

Body-weight in macropodids may fluctuate by a maximum of *ca.* 10% due to variations in the quantities of food present in the stomach and it is doubtful that a given individual could recognize any but relatively large differences in weight between itself and a conspecific, by visual means alone.

The ages of the subjects were not known. F1 and F5 were probably the oldest and youngest adult females and the ages of the males probably corresponded to their numerical order; i.e. M1 was most probably the oldest, M3 the youngest.

5.3 RITUALIZED FIGHTING IN MALE SUBJECTS

5.3.1 Methods

The methods used in recording prolonged interactions between male subjects were the same as those employed in the recording of sexual interactions (Section 4.2.1) and this investigation was carried out simultaneously with the investigation of the latter.

A summary of the behavioural events identified in male-male interactions is presented in Table 5.3.1 and the relevant activities are qualitatively described in Section 5.3.2.

The frequencies of behavioural events identified in agonistic interactions between males for both the dominant and the subordinate individuals involved in each interaction were compared by means of a χ^2 test. Another method sometimes employed for comparing frequencies of behavioural events during interactions is the Wilcoxon matched-pairs signed-ranks test (Croft 1981a,b). The application of this method does not appear strictly appropriate in such analyses as it implies ordination (Siegal 1956) of what, in the opinion of the author, are independent events, in terms of the frequencies of their occurrence. The χ^2 analyses assumed no connection between frequencies of the various behavioural events occurring within given interaction and each event was considered separately.

5.3.2 Inventory and Qualitative Description of Behavioural Events

(a) Approach

All locomotory movements made by a male subject to a position in close proximity to another male were recorded. The initial approach in any interaction was deemed to be the act constituting the initiation and the individual approaching was therefore credited with initiating the bout. Approaches toward an opponents were generally by slow pro-

gression, especially over the final 2 m. Rapid approaches by a dominant individual usually evoked retreat from subordinates and did not result in prolonged fights.

(b) Retreat

All departures from a position of close proximity to another male were scored. The actual termination point of an interaction was not always clear. Animals often simply moved slowly away from each other or commenced some other form of behaviour such as feeding or grooming. Interactions between individuals, with intervening periods of time exceeding 1 min, were scored as separate interactions. In the majority of instances the duration of time between successive interactions was much greater.

(c) Nose-Sniffing (Figure 5.3.1)

This event generally preceded all prolonged interactions between males. After the initial approach during an interaction, the approaching individual usually engaged in nose-sniffing directed at the other animal, which occasionally reciprocated by similar actions. This event also occurred in the course of prolonged interactions.

(d) Genital-Nosing

This event occurred occasionally during male-male interactions. It involved orientation of the head of one individual toward the scrotal region of the other. Whether actual contact occurred during this was difficult to discern; however, this appeared to be the case in many instances. In the course of this event the bodies of both individuals were maintained in a parallel-reverse orientation and the recipient invariably remained motionless during the event.

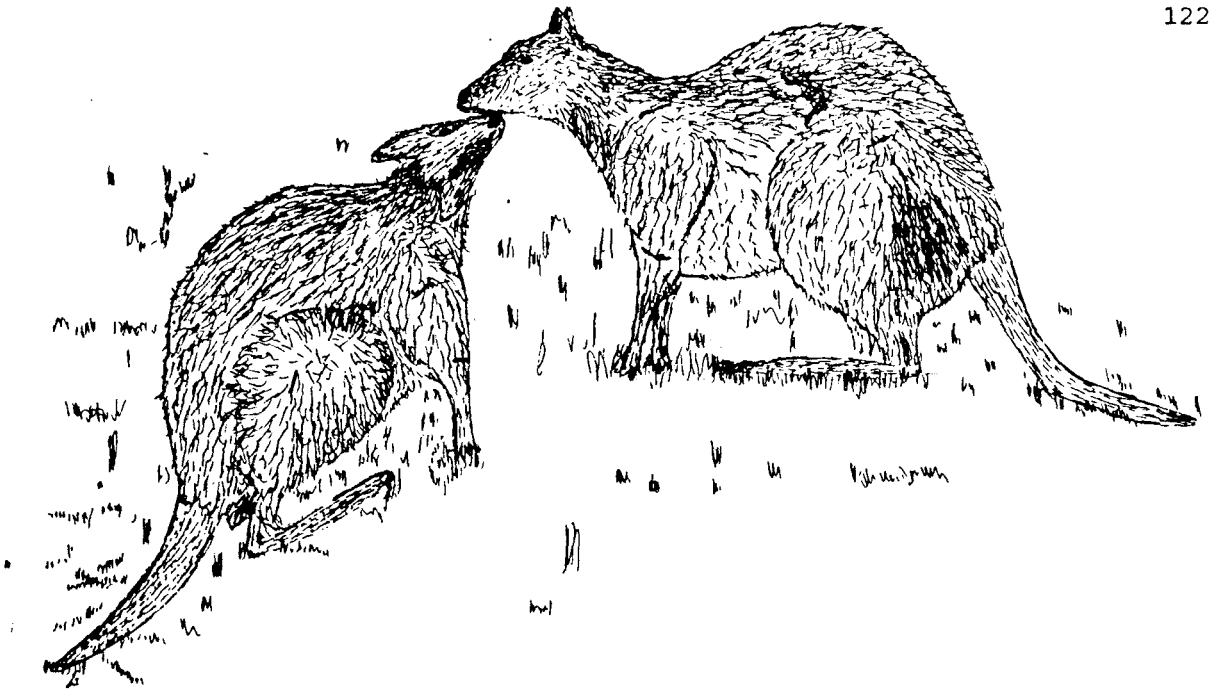


FIGURE 5.3.1: Nose-sniffing

FIGURE 5.3.2: Grappling

(e) Holding

Any form of holding of one individual by another was included in this category. In the majority of cases, individuals held their opponents in the region of the shoulders. Holding was often mutual and in such instances individuals assumed a position similar to that observed in grappling (see below), except that the interacting participants were stationary during this activity.

(f) Grappling (Figure 5.3.2)

Combatants held each other around the shoulders and elevated themselves onto the tips of their toes. They usually hopped back and forth vigorously, or "danced" around in circles. This activity was observed to last up to 30 seconds but the average duration was 5-10 seconds. On three occasions, all three males grappled with each other simultaneously, forming a triangular configuration and in another instance, M3 held onto the back of M1 while it was grappling with M2. This behavioural event appears to be equivalent to the "wrestling" (Croft 1981a,b; Kaufmann 1974a) and "Ringkampf" (Murböck 1975) described in larger macropods.

(g) Kicking

During grappling, one of the combatants occasionally attempted to kick the other in the abdominal region. In the majority of cases it was not possible to discern whether or not contact was made. In the course of this activity both individuals maintained their grip on each other. The tail did not appear to provide any substantial support during kicking.

(h) Push-Down

During the process of grappling, one individual sometimes pushed its opponent over onto its back, then often held it down momentarily before releasing the victim or the latter managed to break loose.

(i) Standing Full-stretch (Figure 5.3.3)

In the course of this event, individuals elevated themselves high, supported one the tips of their toes, with arms outstretched and usually simultaneously hopped up and down. This activity generally preceded grappling and was most frequently performed by M2. It is similar to the "high-standing" posture described by Croft (1981a,b) or to the "Imponierhaltung" (Murböck 1975) of larger macropods.

(j) Push Under and Head Under

Occasionally, an individual grasped its opponent by either the head or shoulders, pushed it downwards and then pulled recipient towards itself so that its head was positioned under its thoracic region. The receipient of these actions sometimes moved forward and "genital-nosed" its opponent. Very occasionally, an individual placed its head under the chest of an opponent without it being actively pushed there (termed head under).

(k) Grasping and Cuffing

These events are largely self-explanatory. All observed incidences of individuals attempting to grasp or cuff their opponent were recorded.

(l) Allogrooming

Occasionally during interactions individuals were observed to groom their opponents. This type of event differed from comparable behaviour observed in male-female interactions in that it was usually

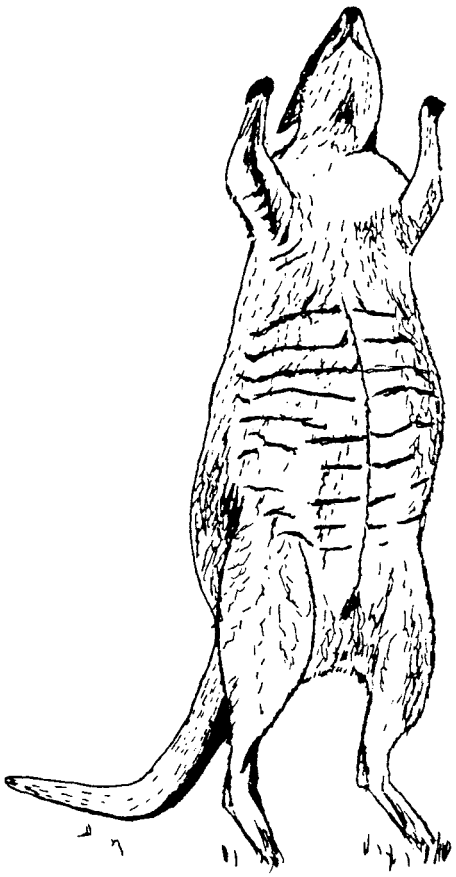


FIGURE 5.3.3: Standing full-stretch

FIGURE 5.3.4: Grass-pulling

directed at the back or nape of the neck of the antagonist rather than at the head region.

(m) Clucking

The clucking vocalization (Chapter 7) was occasionally heard to be uttered by approaching males but from the position of the observer it was difficult to detect. M1 was the only individual heard to make this type of vocalization in this context.

(n) Grooming and Feeding

Behaviours of this type occurring during the course of agonistic interactions are generally considered to be displacement activities (Leuthold 1977). Both these activities were reasonably frequent during male-male interactions and there was no obvious difference in their expression in this context than at other times.

(o) Grass-pulling and Related Behavioural Events

In the grass-pulling activity, the individuals generally extended their bodies and arms horizontally to the ground (Figure 5.3.4) and then retracted the arms, assumed an upright posture and simultaneously grasped and pulled out clumps of grass with the forepaws. The individual performing the action then typically adopted the high-standing posture and threw the tufts of grass against its chest. This sequence was generally repeated several times. Some variations of the expression of the event were observed; e.g. M1 sometimes placed grass into its mouth. Other behavioural events also occurred which are believed to be functionally similar by the present author. M3 was the most aberrant individual in this respect. Occasionally it moved its body back and forth across a fallen branch present in the enclosure, or rubbed its chest against wooden stakes which were positioned around the enclosure (Section 2.1). Another form of behaviour exhibited by

M3 consisted of vigorous splashing of its paws in the container filled with water provided for drinking.

5.3.3 Frequencies of Behavioural Events and of the Interactions Observed

As there was often no clear "winner" of the stylized fights observed, individuals participating in interactions were classed as dominant or subordinate on the basis of the individual's position in the dominance-hierarchy (Section 5.2). The scores obtained for all dominants and subordinates were summed for the sixty interactions scored in detail. A comparison of the frequencies of the various behavioural events observed during male-male interactions in shown in Table 5.3.1.

Dominant individuals initiated interactions (were the first to approach) in the majority of instances and also approached significantly more often during ongoing interactions, whereas subordinates departed with greater frequencies than dominants.

Nose-sniffing was performed with similar frequencies by dominants and subordinates but dominant individuals practised "genital nosing" more frequently than subordinates.

Cuffing, grasping, push-under and standing full-stretch were all events that occurred with significantly higher frequencies in dominant individuals. Dominant subjects were the only individuals observed to score a push-down during grappling. Kicking occurred too infrequently for valid χ^2 analysis; however, in all of the fights scored in detail and in numerous others that were casually observed during the year, only subordinates were observed to kick and kicking almost invariably led to the perpetrator being "pushed-down".

Grooming and feeding were both events that occurred with almost equal frequencies in dominants and subordinates during the course of interactions.

The frequencies of interactions between the three male subjects,

TABLE 5.3.1 Comparison of frequencies of various behavioural events between dominant and subordinate individuals in male-male interactions (χ^2 analysis performed on raw scores).

	Dominant	Subordinate	χ^2
Initiation of bouts	73.3% (44)	26.7%(16)	13.07***
Approach	1.53	0.78	14.56***
Retreat	0.17	1.88	86.25***
Nose-sniffing	0.52	0.43	n.s.
Genital-nosing	0.22	0.05	6.25*
Cuffing	0.13	0.02	5.44*
Holding	0.40	0.22	n.s.
Kicking	0.00	0.08	Invalid
Push down	0.28	0.00	17.00***
Grooming	0.37	0.22	n.s.
Allogrooming	0.13	0.12	n.s.
Clucking	0.05	0.00	Invalid
Grasping	0.47	0.17	8.53**
Feeding	0.40	0.33	n.s.
Other	0.12	0.12	n.s.
Push under	0.23	0.07	5.56*
Grass-pulling	0.22	0.23	n.s.
Standing full stretch	0.23	0.03	9.00**
Head under	0.02	0.07	Invalid
Grappling	0.90	0.90	

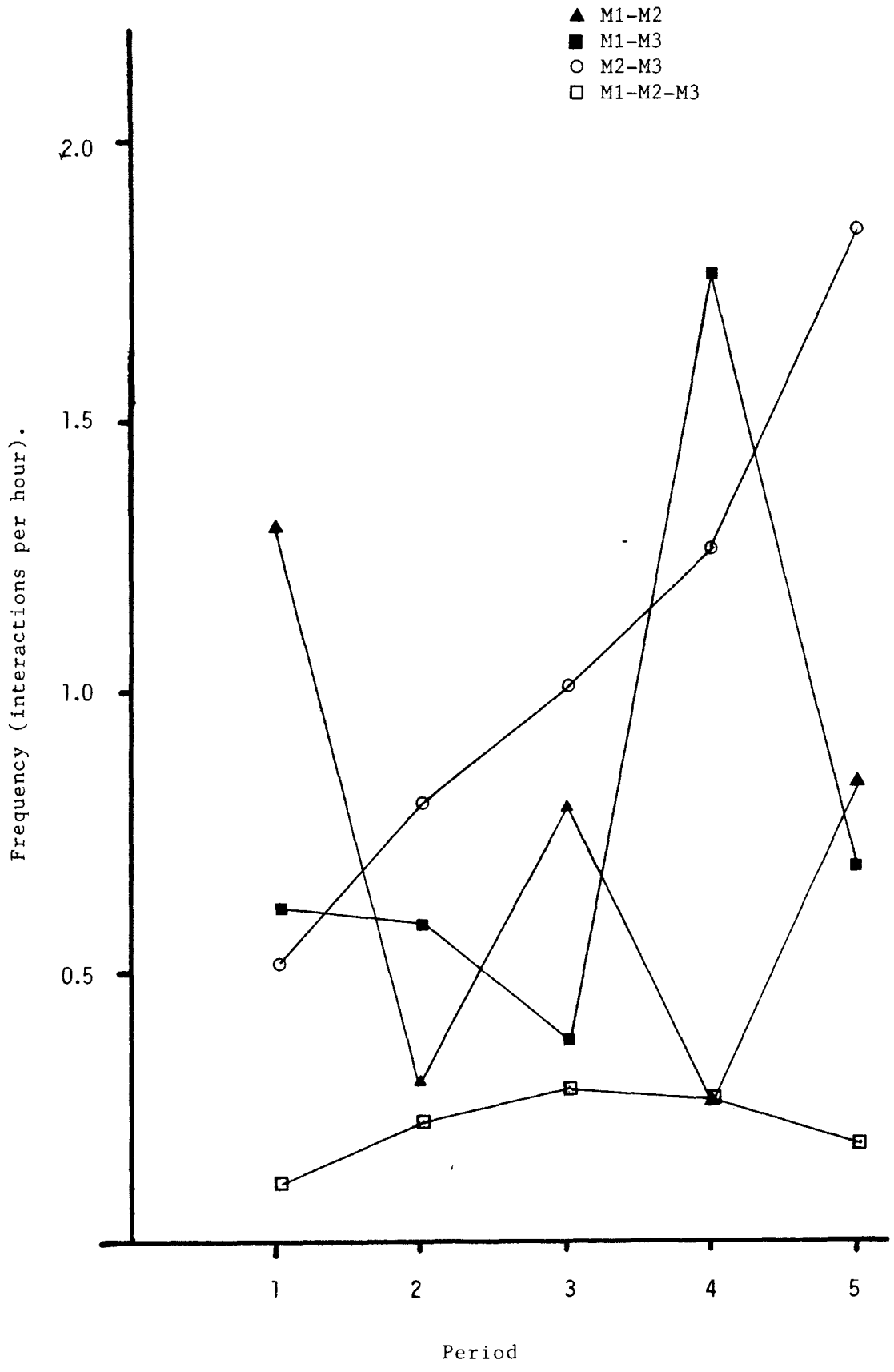
* <0.05

** <0.01

*** <0.001

n.s. not significant

FIGURE 5.3.5: Agonistic interactions between three male subjects of *Thylogale billardierii*.



in five periods of equal length, from the time of the introduction of M2 into the compound until the completion of the study are presented in Figure 5.3.5.

In the first period after the introduction of M2, the latter and M1 interacted frequently but the frequencies of interactions decreased during the next four periods. The frequencies of interactions between M2 and M3 increased markedly over the five periods.

Interactions between M1 and M3 occurred at relatively constant levels over the five periods of observation, except for a greatly increased rate of interaction during period four, the reason for which is not clear. Interactions involving all three subjects were of rather low frequencies throughout the study period.

5.4. DISCUSSION

5.4.1 Social Organization

The overall social organization exhibited by the captive subjects of *T. billardierii* was not hierarchical but within each sex a linear hierarchy generally appeared to exist. In natural conditions, large numbers of *T. billardierii* may congregate at feeding sites but no evidence of a colonial structure or persisting bonds between individuals has been found (Johnson and Rose in press). No investigations of group-sizes have been undertaken to date and most of what is known of the behaviour of this species in natural conditions is based on observations obtained in studies not specifically concerned with this aspect of its biology. The cryptic habits and nocturnal activity of these animals renders field studies of their behaviour difficult.

Hierarchial organization has been reported in many of the species of macropods, both in captivity and in field-studies. Dominance-hierarchies are more commonly and strongly developed in some captive specimens than in free-living conspecifics (Kaufmann 1974a). The fact that in this study there was a constant single food source and one

source of water necessitated, in some ways, a division of the utilization of these items by individuals possibly enhancing some features of the social hierarchy. An important phenomenon noted in this study was that certain individuals were tolerant of some conspecifics but not of others. For example, M1 usually allowed M3 to a much closer proximity to itself than it permitted M2. F3 and F5 fed closer together than they permitted F5 to approach.

Social behaviour in macropods is generally stated to be a less frequent phenomenon than in eutherian herbivores (Russell 1974a) and is certainly less obvious in its manifestations.

The absence of agonistic interactions or tolerance of conspecifics in close proximity is a common type of social behaviour in kangaroos (Kaufmann 1974a; Russell 1974b). Evidence of gregariousness has been noted in many macropods (v. Appendix 4). It appears that *T. billardierii* are reasonably tolerant of their conspecifics, with the exception of males during the time when females are in oestrous (Section 4.4.2). Johnson (1977a) termed the social structure of *T. thetis* monadic, in that individuals did not avoid conspecifics but also did not form any discernible social attachments.

5.4.2 Female-Female Interactions

In this study similarly to the observations of Morton and Burton (1973), female *T. billardierii* exhibit an apparently well-defined hierarchy in captivity. The low level of overt aggressive behaviour exhibited by females is interesting in view of the stability of the hierarchy and raises the question of what maintains the social hierarchy.

Differences in body-size probably play a major role in this respect, especially when the discrepancies are large. However, body-size is not the only factor involved. Dominance by a female over another female may be related to one or only a small number of aggressive acts performed during the initial encounters of the individuals concerned

and subsequently the same individuals may recognize their relative social positions. If this were the case mutual individual recognition by the subjects must be involved. Nose-sniffing was observed to precede supplanting interactions on numerous occasions. If individuals interact with each other with sufficient frequencies, or have well-developed long-term memories of past interactions (this is probably unlikely) a relatively rigid social-structure may be maintained without the need to reinforce this by constant or even frequent fighting.

Low frequencies of overtly aggressive interactions between females has been noted in several species of macropods, *Bettongia lesueuri* (Stodart 1966), *Aepyprymnus rufescens* (Johnson 1980b), *Setonix brachyurus* (Packer 1969), *Macropus rufogriseus frutica* (LaFollette 1971), *M. parryi* (Kaufmann 1974a) and *M.rufus* (Russell 1970a).

Exceptions to the above observations are shown by species in which competition for some important resource is common; e.g. female *M. robustus erubescens* actively compete for resting places in cooler areas (Croft 1981b). Ganslosser (1978) reported vigorous fighting between female *T. brunii;* this involved kicking. Grant (1973) observed similar, highly aggressive encounters between female *M. giganteus;* however, the frequencies of aggressive interactions were low in females of this species (Grant 1974).

Morton and Burton (1973) apparently observed much higher levels of aggression between female *T. billardierii* than was observed in this study. This may be related to the considerably higher densities at which their subjects were maintained (up to 13 individuals in 180 m^2 and 360 m^2 enclosures *c.f.* a maximum of nine individuals in a 440 m^2 enclosure in the present study).

Linear hierarchies have been described in female *M. rufus* (Russell 1970a; Cicala *et al.* 1970) and *M. giganteus* (Grant 1973); and there was some evidence for its existence in *B. lesueuri* (Stodart 1966); however, no social hierarchies were found to exist in female *S. brachyurus*

(Packer 1969, Kitchener 1972) or in *M. rufogriseus frutica* (LaFollette 1971). Kaufmann (1974a) stated that the observed agonistic interactions between free-living female *M. parryi* indicated the existence of recognized dominance-relations between certain individuals but that the frequencies of such interactions were too low to reveal any overall dominance-hierarchy.

Female *Potorous tridactylus apicalis* exhibit near linear hierarchies in captivity; however, the level of aggression observed in female-female interactions is low in comparison to that found in male-male interactions (Buchmann *pers. comm.*).

5.4.3 Male-Female Interactions

Agonistic interactions between male and female pademelons were extremely infrequent, except in the context of sexual encounters when mutual cuffing occasionally occurred (Section 4.2.2). All the overtly aggressive interactions observed involved the adolescent male, M3. In a study of specimens observed in zoological gardens, Morton and Burton (1973) reported a single occurrence of a young male *T. billardierii* chasing a female individual. Johnson (1977a) observed no instances of male-female fighting in a four-year study of *T. thetis*.

LaFollette (1971) reported that aggressive interactions between an immature male and several females were more frequent than those between mature males and females in *M. rufogriseus frutica*. Kaufmann (1974a) observed only one fight between male and female *M. parryi*, involving a subadult male and an adult female.

Croft (1981a) found that female *M. rufus* acted agonistically to male subadults, but not to fully mature males. Packer (1969) observed 16 instances of females chasing subordinate (probably young) males in a study of captive *S. brachyurus*.

Mature males act aggressively toward young females in *Petrogale puella;* this behaviour probably functions to reduce the risk of in-

breeding in this species (Davies 1979).

Low levels of intersexual aggression may be expected in most instances, except in species that exhibit persistent pair-bonding or some other form of similarly rigid social structuring. The vigorous interactions observed between M3 and F5 may have been related to M3 "testing its strength". Fighting between subadult males is often important in the ontogency of their behaviour, enabling them to gain useful experience with low risks of injury. In the absence of other males of similar age, M3 may have resorted to selective harassment of F5, which was of comparable size to it (v. Appendix 1).

The aggression that occurred between F1 and M3 appeared to be related to frustrated sexual advances by the latter individual. At later stages of the study F1 permitted M3 to sexually inspect its cloacal region etc. (Section 4.2).

The apparent success in interactions enjoyed by F6 over M3 is difficult to explain. Individuals often show a higher degree of restraint in their interactions with younger animals. The pugnacity of F6 may have been a factor causing M3 to retreat on many occasions.

5.4.4 Male-Male Interactions

Ritualized fighting between males has been reported in several species of the larger macropods. A summary of various behaviour-patterns observed in male-male interactions in the subfamily Macropodinae is presented in Table 5.4.1. Fighting in male *T. billardierii* resembled in several respects that described in the larger wallabies and kangaroos. The grappling-posture assumed by individuals of this species when fighting has been reported for *T. thetis* (Johnson 1977a) and *T. brunii* (Ganslosser 1978), *Macropus rufogriseus frutica* (La-Follette 1971, Murbock 1975), *M. parryi* (Kaufmann 1974a), *M. giganteus* (Grant 1973), *M. robustus erubescens* (Croft 1981b) and *M. rufus* (Sharman and Calaby 1964; Frith and Calaby 1969; Croft 1981a), but

TABLE 5.4.1 A comparison of agonistic behaviour of species in the family Macropodidae (modified in part from Croft 1982).

*One incident of a male battering a grass tussock.

Species	Behaviour Pattern					Source
	Upright Posture	'Stiff-legged' Walk	'head-toss'	'grass-pulling'	Boxing	
Macropus antilopinus	+	-	+	+	+	Croft 1982
M. robustus erubescens	+	-	-	+	+	Croft 1981b
M. rufus	+	+	-	±	+	Croft 1981a
M. giganteus	+	+	-	+	+	Grant (1974), Kaufmann (1975)
M. fuliginosus	+	+	-	+	+	Coulson (1977), after Croft (1982)
M. parryi	+	+	-	+	+	Kaufmann (1974a)
Wallabia rufogrisea frutica	+	-	-	-	+	Lafollette (1971) Murbock (1975)
Thylogale brunii	+	-	-	-	+	Ganslosser (1978)
T. thetis	+	-	-	±*	+	Johnson (1977)
T. billardierii	+	±	-	+	+	This study
Setonix brachyurus	-	-	-	-	-	Packer (1969)

+ recorded
- not recorded
± rare

apparently does not occur in *Setonix brachyurus* (Packer 1969).

Kicking during grappling is apparently more frequent in the larger macropodids. However, in all carefully observed instances kicks are delivered with a thrust rather than a downward rake with the presumable intent to knock the opponent off balance, rather than to disembowel it (Ewer 1968). Male *M. rufogriseus frutica* may rebound spectacularly from the chest of their opponent during this event (Murbock 1975). Kicking is associated with losing agonistic encounters in *M. parryi* (Kaufmann 1974a) and in *M. rufus* (Croft 1981a) but not in *M. robustus erubescens* (Croft 1982). It appears to be particularly disadvantageous to the individual performing the act in *T. billardierii* (this study), as the tail does not appear to give substantial support; consequently, the perpetrator is almost completely unbalanced during the process of kicking.

"High-standing" (Croft 1981a,b), "Imponieren" (Murböck 1975) or "standing full-stretch" (this study) behaviour have been categorized as a threat display by Kaufmann (1974a) on the basis of Walther's (1974) classification of visual displays. In *T. billardierii* the event standing full-stretch usually results in either retreat by the individual at which it is directed or in fighting between the perpetrator and the recipient, hence it also appears to function as a threat display. It is not, however, as prolonged an event in this species as in the larger macropods and its functional significance as a form of visual display is probably more limited. In this respect it apparently reflects a stage of progression from being purely a transition movement preceding fights (in order to achieve the grappling posture the standing full-stretch posture must be assumed by the combatants) to that of a pronounced threat display such as exhibited in red and grey kangaroos (Russell 1974b).

Grass-pulling behaviour has not been previously described in any of the smaller or medium-sized macropods. It apparently occurs in a

lower proportion of contexts in *T. billardierii* than, for example, in *M. parryi* (Kaufmann 1974a). This event also appears to function asa threat display or possibly a superiority display as it did not necessarily result in the performance of decisive fighting activities.

As was previously noted (Sections 2.2.1 and 4.2.5) macropods often exhibit sexual dimorphism with respect to the thoracic and arm-musculature and it is possible that this behaviour may demonstrate to an opponent the strength of the individual performing it, information that is directly transmitted during grappling behaviour. The development of this display may have occurred from displacement activities or redirected attacks; alternatively it may have been related at some stage to the spreading of glandular secretions of the thoracic region (Kaufmann 1974a). The "bush-display" of *M. robustus erubescens* (Croft 1981b) and the branch rubbing behaviour exhibited by M3 in this study suggest that such activities are in some way related to the spreading of glandular secretions. This behaviour may still function as a display, even in species that have secondarily lost the ability to emit such substances; however, this would mean that the presence of thoracic glands is a primitive (plesiomorphic) condition because it would appear highly unlikely that displays such as these could arise independently in each of the macropodid taxa that exhibit them.

An alternative derivation of such displays may be from feeding behaviour. Feeding and grooming often occur in the context of fights between male individuals of various species of ungulates and in these they appear to be displacement activities (Leuthold 1977). The placing of grass into the mouth shown by M1 may be an indication of such an origin.

Grooming behaviour has become ritualized in *M. rufus* and *M. robustus erubescens* (Croft 1981a,b). This did not appear to be the case in the grooming activities of *T. billardierii* observed in this study; grooming in the context of agonistic interactions may have constituted

displacement activities or autochthonously motivated comfort-behaviour.

The most probable origin of the grass-pulling displays is re-directed aggressive behaviour. Similar behaviours occur in several species of Bovidae, for example "horning or thrashing the ground or shrubs", and is believed in many such cases to reflect an ambivalent state of the performer, i.e. a balance between fear and aggression (Leuthold 1977).

In a documented instance of a display of this nature observed in *M. antilopinus,* the male was described as having an erect penis and to urinate once in a "high-standing" posture (Croft 1982). Male lechwe, *Kobus leche,* often have an erect penis and occasionally ejaculated during "grass-horning" (Robbel and Child 1975).

A single episode of "nosing" of the genital region has been noted in interactions between male *M. rufogriseus frutica* by LaFollette (1971), who classified this as a homosexual act. In *T. billardierii* it was predominantly performed by dominant individuals and may have been a demonstration of superiority by performers.

The absence of any retaliatory reactions by the recipients could possibly be a submissive gesture. Attempts to sniff at the anal region of an opponent occur in *T. brunii* during fights (Ganslosser 1978).

The relationship between "pushing under" and the "head under" events may be similar, the former possibly functioning to assert dominance, whereas the latter may be a form of appeasement activity.

All of these behaviours may be related to the presence of glands in the thoracic and genital regions of the individuals exhibiting them; however, such glands have not yet been described in *T. billardierii*. Johnson (1977) reports of the presence of paracloacal glands in *T. thetis, T. stigmatica, M. rufogriseus, Wallabia bicolor* and *B. gaimardi,* and that those found in *T. thetis* have a pungent odour. Mykytowycz and Nay (1964) have described glands in the sternal regions in several

macropodid species.

Allogrooming performed in the course of fights between males appears to be a fairly infrequent occurrence in most macropods. It has been reported in male *M. rufogriseus frutica* (LaFollette 1971), *M. giganteus* (Croft 1982) and *M. rufus* (Croft 1981a); it is, however, commonly observed in male-male interactions of *M. fuliginosus* and *M. antilopinus* (Croft 1982). In *T. billardierii* male individuals apparently licked their opponents rather than bit it. Such grooming may serve to facilitate the limitation of aggression during fighting or it may reflect a low threshold motivational state for biting.

The ritualized fighting of male *T. billardierii* and of larger macropods appears to incur a relatively low risk of injury for the participants (this study, Ewer 1968; Kaufmann 1974a; Croft 1981b), and in this respect it probably differs from the non-ritualized interactions occurring during the period when females are in oestrous.

The most plausible explanation for the occurrence of such fights is that they assist in the determination of relative social rank. There was often no clear winner in such interactions in *T. billardierii*, as in *M. parryi* (Kaufmann 1974a); however, there were clearly differences in the fighting behaviour of dominant and subordinate individuals. It is likely that dominance in macropods plays a major role in reproductive success of males.

CHAPTER 6

MOTHER-OFFSPRING RELATIONS AND ONTOGENY OF BEHAVIOUR

6.1 INTRODUCTION

The relationship between parents and their offspring is one of the more obvious and important aspects of the social behaviour of mammals. The unique morphological and reproductive adaptations of marsupials renders this facet of their biology particularly interesting. In most macropods, as in the eutherian ungulates, care of the offspring is apparently almost completely the responsibility of the mother.

Closely related to investigations of parent-offspring interactions is the study of ontogeny of behaviour. Parental care is an important component of the early environment of the young and the interactions between parent and offspring are often virtually essential in enabling the young to adjust to its physical and social environment (Russell 1973).

Aspects of mother-offspring interactions and early ontogeny of behaviour have been described, to date, in *Macropus rufus* (Russell 1970b, 1973; Croft 1981a), *M. robustus erubescens* (Croft 1981b), *M. giganteus* (Grant 1974), *M. parryi* (Kaufmann 1974a), *M. eugenii* (Russell 1973), *Thylogale thetis* (Johnson 1977a), *T. billardierii* (Morton and Burton 1973), *Setonix brachyurus* (Kitchener 1972) and *Aepyprymnus rufescens* (Johnson 1980b).

During the course of other studies some information was collected incidentally on the ontogeny of behaviour and mother-offspring relations of a single specimen of *T. billardierii*. In view of the lack of information pertaining to this area of research in macropods, the relevant data is presented below.

Russell and Nicholls (1974) found that distress vocalizations of young *M. rufus* are individually specific. They suggest that females may be able to discern such differences and use them for identifying their offspring. Calls of individual young *T. billardierii* also exhibit apparent differences (Section 7.3) and it was, therefore, hypothesised that

females may be able to recognise the calls of their own young. In order to test this hypothesis, a series of playback experiments were performed and the possibility that young may recognize the calls of their mothers was also investigated.

6.2 ONTOGENY OF BEHAVIOUR

6.2.1 Methods

During the investigation of diel activity-patterns, information pertaining to the development of behaviour of subject F6 was incidentally collected. Casual observations before and after this period yielded additional information in relation to such behaviour.

Cursory observations were also made on subjects M4 and M5 in various stages of their pouch life. M4 died two days after it was first observed to leave the pouch.

In order to estimate the ages of all pouch-young used in this study, the method of Rose and McCartney (1982b) was employed which relates head length of the young to its age. This method was found to be most accurate; test on pouch-young of known ages were found to yield calculated estimates to within *ca.* 2 days of the actual ages.

6.2.2 Results

(a) Early Pouch-life

F6 and M4 were first observed with their heads protruding from the pouch at 134 days and 140 days-old, respectively. In the majority of early incidences of this event, it generally occurred during the time when the mother was grooming the pouch-region and the young retracted its head after only *ca.* 30 s. At later stages of its development, particularly when the mother was moving about and feeding, the young protruded its head intermittently during most of a 2 h observation session.

After *ca*. 2 weeks from the time when the young were first noted with their heads protruding from the pouch, they were observed to nuzzle the ground; it is doubtful that they were actually eating grass at this stage as their jaws did not appear to move. Within a week thereafter clearly defined nibbling movements were seen; however, whether or not grass was ingested during this process cannot be stated. At times when the heads of young protruded from the pouch the mother was occasionally observed to lick it around the exposed regions, and presumably also groomed the rest of the body, while cleaning the pouch.

(b) Interim Pouch Life (young out of the pouch for short periods)

The first observed excursions from the pouch by F6 and M4 occurred when they were 177 and 166 days old, respectively. In the first observed episode of F6 leaving the pouch, it was outside the latter for 50 min; it was therefore probable that this was not its first excursion. However, M4 apparently fell from the pouch on the first occasion it was seen outside and immediately attempted to return to the pouch, which it succeeded in doing after *ca*. 1 min.

During the period before it vacated the pouch permanently, F6 remained in close proximity to its mother, F5, on its excursions from the pouch. However, it periodically dashed to distances of a few metres from its mother, then quickly returned. The time in the pouch decreased gradually over the period of the interim pouch life. However, this decrease was very slow in comparison with the abrupt change at the termination of the pouch life. A regression of the time spent in the pouch over eight successive 4 h sample periods obtained during the interim pouch life revealed no clearly defined trend; $Y = 11.00 - 0.667X$ ($r^2 = -0.65$, $0.10>Pr>0.05$; $F_{1,7} = 4.45$, $0.10>Pr>0.05$). However, this was probably because of variation due to the fact that F6 and F1 were not visible at all times (v. Section 3.2), consequently the time spent in the

pouch, and the time sojourning outside it may have been greatly underestimated in some of the sample-periods. A graphical representation of the number of scan-samples during which F6 was observed to be in the pouch in the eight observation periods is shown in Figure 6.2.1. In addition the time during which the head of F6 protruded from the pouch is indicated (data for these analyses were collected during the investigation of diel activity-patterns, Section 3.2).

(c) Changes in Time-budgets with Age

The time-budgets obtained for F6 over the four-sample days (Section 3.2) are shown in Table 3.3.21. From these it is apparent that by "day 4", F6 spent amounts of time engaged in most activities comparable to adult individuals. F6 was 210-240 days old at this stage. After vacating the pouch, until the time of weaning, F6 suckled for about 20 min per day. It must be noted in this context that suckling was scored as the time F6 had its muzzle in the pouch. Russell (after Grant 1974) observed young of *M. eugenii* with its head in the pouch of a female that was known to have no milk. Although the activity was not continuously monitored F6 (age *ca.* 280 days) was observed to suckle from F1 for 12 mins one week before the mother began to act aggressively towards it (Section 6.3).

(d) Play

The problem of defining play is a contentious issue in ethology. It is common practice to include in this category behaviours to which no direct function can be attributed with certainty or in which the motivational state of the animal performing a particular type of activity cannot be readily inferred. The ensuing description of behavioural events is presented by the author as possibly pertaining to play behaviour, based mainly on subjective criteria.

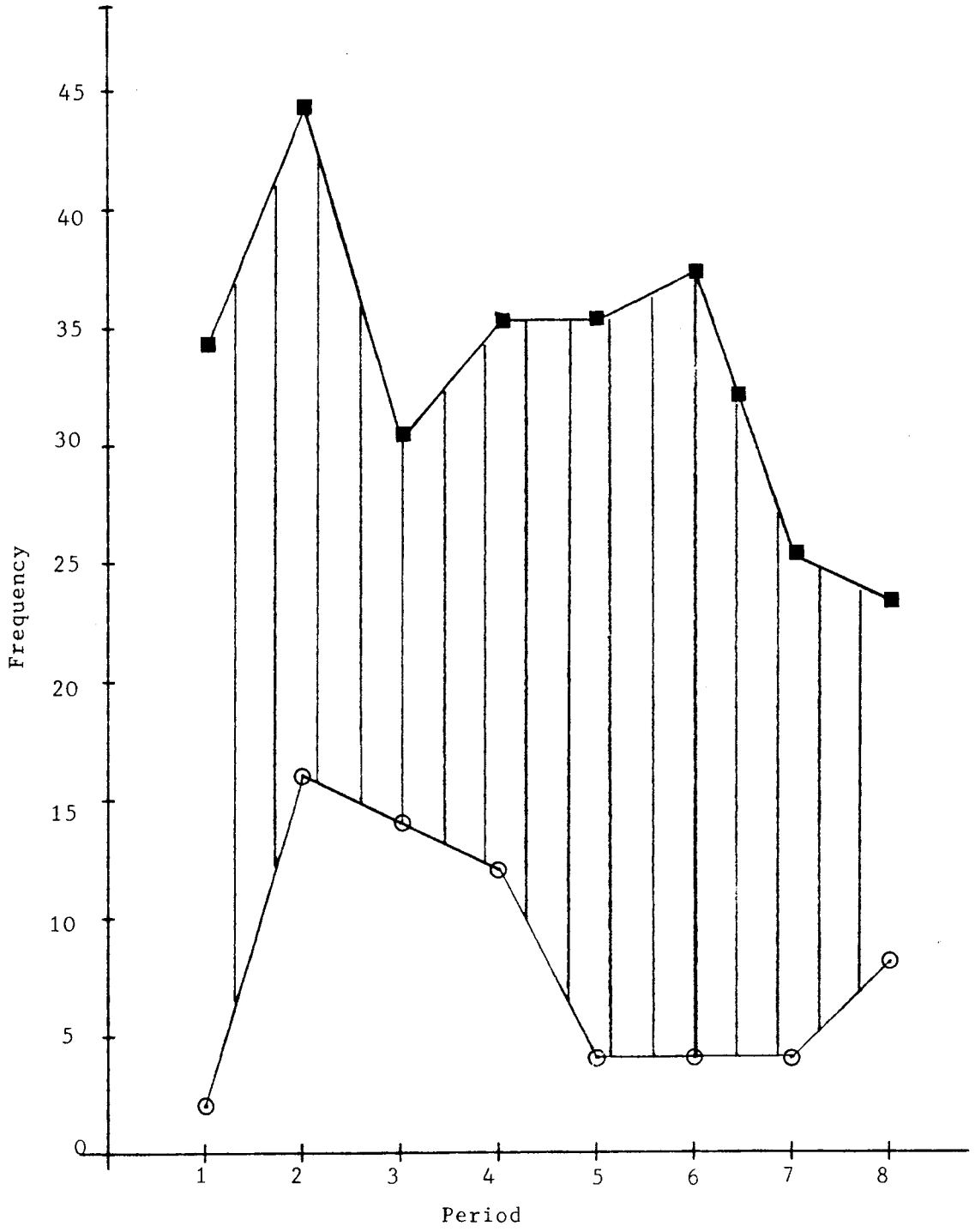


FIGURE 6.2.1: The frequency of scan-samples where F6 was recorded as being in the pouch (■) during eight sucessive 4h (2h+2h) sampling periods. The proportion of scan-samples where F6 had its head protruding from the pouch is indicated by the lower line (○).

The most common form of play behaviour consisted of rapid hopping around in circles for periods ranging from 30 s to 5 min. This type of behaviour was most commonly observed in the late afternoon (*ca.* 1600 h). The total distance traversed during this activity was usually only *ca.* 5 m.

Two other forms of activities that may be classified as play behavious were observed. On a single occasion (2/7/82), F6 was observed to make exaggerated digging movements and in the process it scattered dirt and dead leaves in various directions. This activity continued for about 20 s. The other instance observed was of F6 vigorously pulling and biting on a piece of hessian that was attached to a section of the fence (2/7/82).

Apart from interactions with its mother, F6 (Section 6.3) often engaged in social activities with other animals in the enclosure, especially with M3. Its behaviour in episodes involving this individual often bore several of the characteristics of the ritualized fighting behaviour of male subjects (Section 5.3), except that they were more abbreviated and perfunctory in nature. The following summarised protocol represents a typical interaction between F6 and M3: "27.7.82, 0610 h - F6 approached M3 then reared up to assume the standing 'full-stretch' posture; cuffed M3; both individuals grappled briefly; M3 retreated". These behaviours were classified as play because subjectively evaluated they did not appear to be "in earnest"; although this is based on highly arbitrary criteria, it is one that is commonly used in characterising play behaviour (Ewer 1968; Hinde 1970).

6.3 MOTHER-OFFSPRING INTERACTIONS

6.3.1 Methods

The following descriptive account is based on observation-sessions that occurred during the year, as outlined in Sections 3.2 and 4.2.1 and

on other, non-systematic observations performed throughout the course of the study. Subjects were examined on at least every third night to ascertain which individuals were resting together (Section 2.3).

6.3.2 Inventory and Qualitative Description of Events

(a) Allogrooming (Plate 6.3.1)

This was of common occurrence in mother-offspring interactions and was mutually performed in the majority of observed instances. From the study of activity-cycles it was found that the frequencies of bouts of allogrooming practised by F6 were highest on the second sampling "day" which corresponded to the later half of its interim pouch life (Table 3.3.21). F1 allogroomed for an average of 46.75 min per day (Table 3.3.20) and although a part of this activity was directed at M1, the great majority of the total allogrooming effort of F1 was directed toward F6.

In general, allogrooming actions performed by both individuals were concentrated around the head region, especially the muzzle of the recipient. However, F1 groomed almost all of the body of F6 when the latter was younger.

(b) Resting Together (Plate 6.3.2)

F6 and its mother, F1, rested together during all observed bouts of nocturnal resting until the stage when F1 began to act aggressively toward F6; however, during the daytime F1 and F6 usually rested separately, typically in different sectors of the enclosure (Figure 3.3.3, Table 3.3.16). The resting-together position was the same as that of adult males and females (Section 2.3).

(c) Pestering

This behaviour was similar to that described in *M. rufus* (Russell

PLATE 6.3.1: Allogrooming

PLATE 6.3.2: Resting together

1970b). It generally involved pushing and pulling by F6 at the head region of F1 while the latter was in a seated position or standing erect. This behaviour often assumed some of the features of an agonistic interaction, with mutual cuffing occurring between the two individuals. However, such events in this context were apparently gentle and were probably not intended to injure.

Pestering behaviour did not appear to be directly related to attempts by F6 at gaining access to the pouch for purposes of re-entry or suckling. The only occasion when F1 was observed to deny F6 access to the pouch region was on the day when F1 gave birth to a new pouch-young and the opening of the pouch had contracted markedly. This corresponded to the termination of the interim pouch-life of F6 (this probably occurred prematurely because of the effect of the bromocriptine experiment v. Appendix 3).

(d) Communication

Vocal communication between mother and offspring is reported in Section 6.5. In addition to this, olfactory cues were apparently important in mother-offspring relationships. F1 and F6 were frequently observed to direct sniffing activities at each other. These were usually concentrated around the region of the snout (v. nose-sniffing, Section 2.3).

(e) Weaning

F1 was first observed to act aggressively towards F6, when the latter was 288 days old. Three times within a single observation period (2 h), F1 was observed to attack F6, once chasing it for some distance. F6 was not seen to suckle from F1 after this occasion; however, on the same night and two nights later they were noted to be resting together. After this time, F1 and F6 were not observed to do this and all subsequent

interactions between the two individuals were of a similar form to other observed dominant-subordinate interactions (Section 5.2).

(f) Other

On a few occasions, F1 was observed to intervene in interactions involving F6 and other individuals during the period from when F6 first ventured out of the pouch to its weaning. Such episodes usually involved interactions between M3 and F6 and in these instances F1 approached the two individuals while they were fighting. This resulted in either M3 retreating or F6 moving towards F1. Although it was not always possible to establish, F1 apparently uttered the clucking sound during these incidents.

On a single occasion F6 was attacked by F5. F6 uttered the hissing vocalization as it retreated and F1, which was feeding at a distance of *ca*. 3 m from the former, approached rapidly to the locality previously occupied by F6 and F5. F1 followed after F6 and the latter individual initially continued to move away from its approaches. A few minutes later, F6 rushed rapidly at F5, halted *ca*. ½ metre short of it then moved back quickly to where F1 was feeding.

These incidents were typical of the interactions occurring between F6 and F1 during the period up until weaning. However, F1 did not react in any distinctive way when M1 sexually investigated and courted F6 (Section 4.2) despite the fact that F6 often moved very close to F1 during such interactions.

6.4 MAINTENANCE OF SPATIAL PROXIMITY

6.4.1 Methods

Collection of data relating to the maintenance of spatial proximity and the methods of analysis used in assessing the role of mother and

offspring in this context were the same as those outlined in Section 4.3.1, *viz.* All approaches and departures of F1 into and from a quadrat in which F6 was present and the reverse events were recorded (AQm = approach by mother, AQi= approach by infant, LQm = departure by mother, LQi = departure by infant). Similarly, approaches and departures by the subjects from positions of close proximity to each other were recorded, i.e. when actual contact between F1 and F6 could or did occur (ANm, ANi, LNm, LNi).

As only two individuals were considered, χ^2 analyses were performed on the basis of the hypothesis that AQm = AQi, LQm = LQi, ANm = ANi and LNm = LNi. In addition, the original formula recommended by Hinde and Spencer-Booth (1968 after Hinde and Atkinson 1970) was used to calculate *m.p.* values (v. Section 4.3.1).

6.4.2 Results

The observed frequencies of approaches and departures by F1 and F6 in the context of the two types of spatial relationships specified are presented in Table 4.3.1. The results of χ^2-analyses are also shown.

TABLE 6.4.1 Observed frequencies of approaches (AQ) and departures (LQ) into and from a quadrat occupied by one individual, by a mother and its infant and approaches (AN) and departures (LN) from adjacent positions, of the two individuals. Expected frequencies shown in parenthesis.

	Mother (F1)	Infant (F6)	χ^2	P
AQ	9 (23.5)	38 (23.5)	17.89	<0.001
LQ	17 (22.0)	27 (22.0)	2.27	n.s.
AN	2 (14.5)	27 (14.5)	21.55	<0.001
LN	13 (13.5)	14 (13.5)	0.04	n.s.

The differences between percentages of approaches by the infant and departures by the infant (a) into and out of the quadrats occupied by its mother yields a *mp* = +17.78, and (b) to and from a position immediately adjacent to its mother yields a *mp* = +37.93.

It is apparent from the results that F6 approached F1 with much higher frequencies than those with which the reciprocal event occurred, in both of the spatial relationships ("quadrat" and "immediately adjacent") examined. However, both individuals moved away from each other with comparable frequencies. Similarly, the high positive values of *mp* obtained for each of the spatial criteria indicate that it was F6 that was primarily responsible for maintaining spatial proximity to its mother, F1. However, the *mp* value calculated for quadrats was only half of that obtained for close proximity, indicating that at greater distances the mother played a more active role in maintaining proximity to its young.

6.5 RECOGNITION OF CALLS

6.5.1 Methods

The methods of obtaining vocalizations of mothers and their offspring are outlined in Section 7.2. For the purposes of play-back experiments, continuous loops of tapes of calls were constructed. During the initial trials, involving F1 and F6, recording and playbacks were performed in the open. During later trials, the author and the tape-player used were situated within the observation-room and a lead was extended to a speaker situated on the ground *ca.* 2 m from the front wall of the shed. The actual conditions of the playback trials are shown in conjunction with the results.

The positions of all subjects within the enclosure were noted at the commencement of each trial and any identifiable reactions to the playing of the tape was recorded. Tape-loops were played continuously for 2 min in all trials performed in the observation shed. Details of the

calls recorded for playback are presented in Table 7.2.1. During the initial trials, tapes were played for variable lengths of time but generally for less than 2 min.

6.5.2 Results

On the 26.4.82, F1 was captured in order to check the age of its pouch-young F6 (=155 days old, v. Appendix 1). When F1 was released, F6 fell from the pouch as its mother moved away from the author and assistants. F6 then immediately began to utter the hissing vocalization. F1 moved toward F6, emitting the clucking vocalization as it approached. F4 approached toward F6 and F1 moved rapidly toward the former, causing it to retreat. When F6 and F1 reached each other, F6 was noted to have some difficulty in locating the pouch and *ca*. 2 min elapsed before it was able to regain its position therein. During this process, F1 remained motionless and made no attempt to aid F6 in its efforts to return to the pouch. Similar observations were noted in subsequent separations of pouch-young from their mothers. However, on one occasion (30.11.1982), subject M5 (age 182 days) which had been separated by the author from its mother, F1, for some time (*ca*. 1 h) ran straight to the thicketed region of the enclosure after its release (Figure 2.1) and remained motionless there, until F1 commenced to utter the clucking vocalization when M5 began to produce distress calls and mother and offspring approached each other.

It was initially intended to pursue a series of playback-experiments using F5; however, its pouch young (M4) died soon after it was first observed to venture from the pouch (v. Appendix 1). Consequently, only one series of trials was performed on the day after M4 was discovered dead. Other experiments were undertaken at a later stage and these involved F1 and M5 but time-limitations precluded attempts at more extensive trials. The results of playback-experiments are presented in Table 5.4.1.

TABLE 5.4.1 Results of playback-trials.

Date	Call played	Notes	Reactions of subjects
31.5.82	F6 (age 166 days)	F6 (age 190 days) permanently vacated pouch on this day. M1, M3, F1, F3, F4, F5, F6 present in enclosure. Tape played in the open.	F1 approached to *ca.* 1 m to investigator and tape-player; M1 uttered gutteral hiss once.
"	F1 (clucking)	"	F6 approached to *ca.* 1 m to investigator and tape-player.
1.9.82	F6 (age 166 days)	Tapes played for 2 min, at 2 min intervals M1-3 and F1-6 present in enclosure (player situated in observation room)	F1, which was initially in a seated position, stood erect after 30 s, sniffed air for 10 s then resumed seated position after 1 min 30 s.
"	F1 (clucking)	"	No observed reaction from any subject.
"	F6 (age 323 days)	"	M1, M2 both approached to within 5 m of speaker, then resumed feeding.
"	F6 (age 166 days)	"	F1, F6 5 m away from speaker, no overt responses; F1 occasionally looked in the direction of enclosure and sniffed at F6 several times.
2.9.82	"	"	No observed reaction from any subject.
"	F1 (clucking)	"	"
10.9.82	"	As above, 1 day after M4 (F5 young died)	M1 approached observation-shed.
"	F6 (166 days)	"	No observed reaction from any subject.
"	M4 (155 days)	"	F5 (seated) approached from 20 m to 10 m then commenced feeding.
"	F6 (166 days)	"	No response from F5 (10 m away). F1 sniffed the air occasionally.
"	M4 (155 days)	"	F5 (5 m away) approached very close to the speaker and sniffed.
"	F6 (166 days)	"	F5 (5 m away) occasionally stood erect and pricked up its ears.
"	M4 (155 days)	"	No observed response from any subject.

TABLE 5.4.1 (continued)

Date	Call played	Notes	Reactions of subjects
10.9.82	F6 (166 days)	As above, 1 day after M4 (F5 young) died.	No observed response from any subject.
"	M4 (155 days)	"	"
"	F6, M4 alternately	1 h after the last trial above.	"
30.11.82	F6 (166 days)	M2, F1, F2 present in enclosure, M5 (182 days) removed from F1 and placed in a room outside enclosure.	F1 approached, checking and sniffing the air, to *ca.* 2 m, then moved away.
"	M4 (155 days)	"	F1 sniffed the air, made intention movements to approach*, tail moving up and down.
"	F6 (166 days)	"	F1 moved 4 steps closer to speaker then stopped, still sniffing the air.
"	M4 (155 days)	"	Same response as to the previous playing of this call.
"	F6 (166 days)	"	F1 showed no reaction for 1 min, then approached 4 steps and halted.

* v. Text.

F5 did not appear to react to calls from the young of F1 but did show some responses to the calls of her own young, M4. F1 reacted to the calls of other infants when its pouch young was removed. It was unfortunate that no taped call of M5 could be obtained because judging from previous trials, the response of F1 did not appear to be as strong as its reactions to the call of F6 during the pouch life of the latter individual. It is interesting to note that F1 exhibited much stronger responses to the call of F6 (its previous pouch young) during this trial than to that of M4 (the pouch young of F5), especially during the first two playbacks. Her only response to the call of M4 consisted of sniffing in the air and occasionally raising one foot, then the other, performing movements as if it intended to approach.

The results of these experiments indicate that olfactory cues may be the most important factor in the recognition of young by their mothers. Females constantly sniffed in the air or at their own young if it was present during the playing of juvenile distress calls. Although lacking conclusive proof, the results suggest that females can identify the calls of different young.

By contrast, young reacted to any clucking vocalizations, e.g. all young could be induced to approach quite close to the author when he mimicked the clucking sounds. Females did not show any discernable response when the author attempted to imitate distress-calls of the young, but this may have been due to the poor quality copy of the vocalizations produced.

6.6 DISCUSSION

Rose and McCartney (1982b) reported that pouch young of *Thylogale billardierii* first protruded their head from the pouch at between 151 - 161 days and this corresponded closely to the achievement of a complete coverage of fur over the body. Although the two young observed in this

study were first noted to protrude their heads at *ca.* 2 weeks before the age estimated by the former investigators, these events were of very brief duration and it was not until the 150-160 day period that frequent exposure of the head was seen.

Russell (1973) reported that *Macropus eugenii* were first observed with their heads out of the pouch between ages of 168 - 175 days and, similarly young *M. rufus* (Sharman and Calaby 1964) were first noted to protrude their head from the pouch at *ca.* 150 days of age. Therefore, in these two species and in *T. billardierii* (this study) this event occurs after approximately two-thirds of the duration of the total pouch life.

The behaviour of *T. billardierii* during pouch life is similar to that described in *M. rufus* (Russell 1970b, 1973; Croft 1981a), and in *M. eugenii* (Russell 1973); however, more quantitative studies need to be undertaken to confirm the relationship to other macropods of this aspect of behaviour.

The "running in circles" type of activity observed in F6 has been described in *M. giganteus* (Grant 1974), *M. rufus* (Russell 1970a), *M. robustus erubescens* (Croft 1981b) and *M. parryi* (Kaufmann 1974a); this activity usually takes place in proximity to the mother.

Fighting behaviour is common in young male *M. parryi* but not in young females of this species (Kaufmann 1974a). The behaviour exhibited by F6 toward M3 appears peculiar in this respect and such agonistic interactions between young female individuals and much older animals have not been described to date in any other study of the behaviour of macropods.

Mutual allogrooming between mother and offspring appears to be almost universal and of frequent occurrence in the macropodines (Croft 1982), although it has not been reported in the potoroine marsupials. Female *Potorous tridactylus* do not groom their young after the latter have vacated the pouch permanently (Buchmann *pers. comm.*). In the majority of

recorded instances of allogrooming in macropods it is the mother that most often performs this activity in mother-offspring interactions. Although the cleaning of the recipient is probably an important function of allogrooming, especially of a mother towards its young, allogrooming may also be important in consolidating or re-inforcing the mother-offspring bond, particularly with respect to providing cues that may serve to facilitate recognition of the other individual. Another possible function may be the transfer of microbial bacteria and protozoans which are important in the digestive systems of macropods and which young individuals do not possess at birth (Croft 1981s). The concentration of the grooming of the young around the muzzle-region of the mother appears to support this hypothesis; however, such a localization of grooming effects may also be expected if it is functioning to facilitate recognition.

The resting-together behaviour of a female and young-at-foot observed in this study may represent a behavioural adaptation for conserving body-heat. Younger animals may be expected to be more susceptible to the adverse effects of lower temperature; and their smaller sizes presumably pose greater problems of thermoregulation. Resting in contact may be common in macropods maintained in zoological gardens in areas exposed to cold climates (Schürer 1978 after Ganslosser 1980*).

Varying degrees of aggression toward pouch young at the time of their weaning have been reported in *T. billardierii* by Morton and Burton (1973). Such aggression is, apparently, uncommon in most macropods. The presence of another pouch young may encourage the earlier and more rapid onset of weaning.

In all macropods in which the process has been investigated, the young appear to be primarily responsible for maintaining spatial proximity to the mother (Russell 1973; Croft 1981a,b). Johnson (1977a) believed

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* In the absence of the original paper, the present author presumed Schürer's (1978) study was undertaken in European (probably German) zoological gardens.

this also to be the case in *T. thetis* and it is probably so in *M. parryi* (Kaufmann 1974a). Changes in the relative roles of mother and offspring with respect to the maintenance of proximity over different distance regimes were not investigated in these studies and the results obtained in this study indicate that such relationships are not necessarily static. Future research on this aspect of mother-offspring relationships may be useful.

Although the experiments made on recognition of calls were not conclusive, the results give some credence to the possibility of mothers being able to recognize the vocalizations of young individuals as emanating from their own offspring. Experiments in simultaneous dual playbacks from different points in an enclosure may be useful and variations with the ages of the young in relation to maternal responses should also be investigated. Mutual recognition of vocalizations has been reported in mother-offspring dyads of reindeer, *Rangifer tarandus tarandus*, (Espmarck 1971) and a substantial amount of circumstantial evidence pertaining to this has been reported in several other species of ungulates (Lent 1971).

CHAPTER 7

VOCALIZATIONS

7.1 INTRODUCTION

Macropods appear to have a limited repertoire of vocalizations (Kaufmann 1974a); nevertheless, acoustic communication still plays an important role in the behaviour of various species, e.g. in mother-offspring relationships (Section 6.5.2). The majority of behavioural studies reported to date on macropods included descriptions of all of the vocalizations identified; however, analyses of call-structures have only been performed on distress vocalizations made by young *Macropus rufus* (Russell and Nicholls 1974).

Morton and Burton (1973) described some of the vocalizations of *Thylogale billardierii* but limitations imposed by conditions of their study prevented some vocalizations, e.g. those of pouch-young, from being detected.

The aims of this section of the study were:

(a) to describe the acoustic features of calls identified in *T. billardierii* and, if possible, relate these to their presumed functions;

(b) to determine if there is any variation in calls of similar types between different individuals and with different ages of the same individual.

Due to limitations of time, numbers of suitable subjects and other factors, this study was essentially cursory in nature and the need for further investigations on this aspect of the behaviour of *T. billardierii*, and that of macropods in general, must be emphasized.

7.2 METHODS

Throughout the period of the study vocalizations that were detected and the contexts in which they were emitted, were systematically noted.

Recordings of as many of the identified calls as was feasible were

collected. Vocalizations were recorded on a Philips reel-to-reel (Tape speed 7 3/4 inch 5^{-1}) using a Nakamichi direction microphone (CM300, 20052). For the purpose of recording calls of mothers and their offspring, females were captured, their pouch-young were then removed and placed in a small wire compound situated in one corner of the enclosure (Figure 2.1). While separated, both mother and offspring vocalized almost continually permitting the relevant recordings to be made.

The author was unsuccessful in obtaining taped recordings of the "hiss-growl" made by pademelons during agonistic encounters, due to its infrequent occurrence and difficulties in approaching sufficiently close to the source of the sound to produce adequate recordings. It was noticed that during handling, *T. billardierii* uttered a vocalization that sounded very similar to this growl, therefore recordings were made of the calls uttered while the subject was held by the tail with the aid of an assistant and mildly harassed (generally, simply touching the subject on the back was sufficient to elicit a growl).

Similar problems were encountered in attempting to obtain records of the "clucking" vocalization of males. However, while one male was consorting with an oestrous female (Section 4.4.2), it emitted this vocalization quite frequently and the author was able to position himself in sufficiently close proximity to the subject. Unfortunately, the original recording equipment was not available at this stage of the investigation and it was necessary to use a standard cassette-recorder (National) for recording; there was also a relatively large amount of background noise during the proceedings. Consequently, the quality of recording was, in many respects, inadequate. Details of the individual records of calls are shown in Table 7.2.1.

Continuous tape loops were constructed of each of the calls recorded and these were analysed by two methods: (a) an oscilloscope (Tektronix 5030 dual beam) was employed to produce time-amplitude traces (oscillo-

TABLE 7.2.1 Details of recording the vocalizations used in analyses. See the text for elucidation.

A - adult
* - Output of graphic equalizer

Subject	Age	Date of Recording	Behavioural Context	Filters employed in the production of oscillograms	Gain* (Oscillo-graph)
M4	155 days	1.9.82	Separated from mother	250 Hz - 16 kHz	20 db
F6	166 days	5.9.82	"	"	"
F6	323 days	20.9.82	Harassment	"	"
F2	A	1.9.82	"	500 Hz - 2 kHz	40 db
F4	"	20.9.82	"	250 Hz - 16 kHz	20 db
M1	"	27.9.82	When consorting with female	1 - 16 kHz	40 db
F1	"	5.9.82	Separated from young	"	20 db
F5	"	1.9.82	"	"	"

grams) of the calls, which were then phographed. Output from the tape-player was directed to the oscilloscope via a variable band-pass filter (Jaycar graphic equalizer); this was employed to eliminate spurious background noises. Filters employed in the production of each oscillogram are shown in Table 7.2.1. (b) Sonograms of representative vocalizations were produced by a "sonograph" (Kay Electric Company, New Jersey). Only samples of vocalizations 2.4 s or less, in duration could be analysed at any one time. A narrow frequency band-pass filter (45 Hz) was employed in all cases and mode FS-1 was used for the frequency-response setting, as this provides a better linear response with changing frequencies. The sonograms produced yield information about the time-frequency of the sample considered.

More detailed information on these methods of analyses has been given in Greenewolt (1968), pp.7-12.

7.3 RESULTS

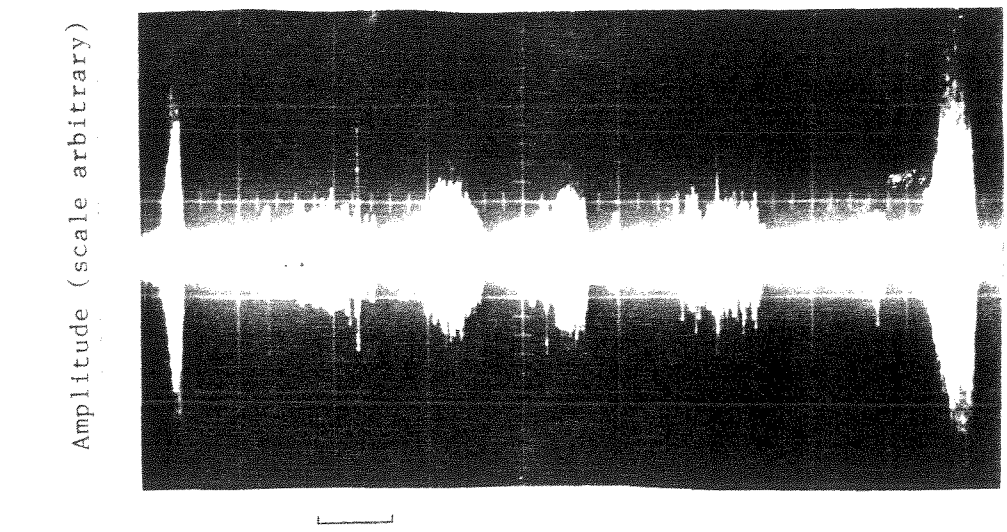
The sonograms and oscillograms produced from calls of two young *Thylogale billardierii* (F6, M4) are shown in Figures 7.3.1 and 7.3.2. The vocalizations of each subject comprised two distinct types of chirp (terminology after Broughton 1963), (a) a brief (*ca.* 100 ms duration) chirp of large amplitude and (b) a longer (*ca.* 200 ms duration) chirp of smaller amplitude. To the human ear, these chirps resemble a "Shhh..." and "Shhhuht" sound, respectively. All of the frequency-ranges of analyzed chirps obtained for both M4 and F6 were wide (0-9 Hz); however, the individual frequency-distributions were different in each subject. Chirps of M4 exhibited three distinct frequency-bands (positions in which greater amplitude was evident) at *ca.* 1, 4 and 7 Hz, whereas the distribution of frequency-amplitude of individual chirps of F6 were, in general, more homogenous although some banding was also apparent at *ca.* 1, 2 and 4 Hz.

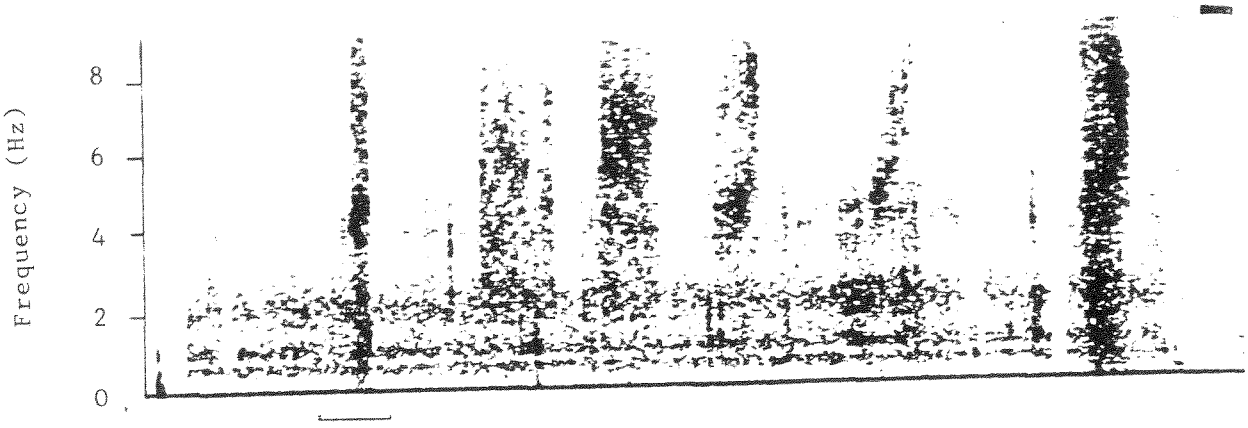
The call of subject F6 at a later age is shown in Figure 7.3.3. At this stage, it had permanently vacated the pouch and the calls were obtained by the "harassment" method. There are obvious differences between this call and the previously mentioned one. The duration of each chirp was much longer (500 ms and 1200 ms, respectively). The frequency-distribution of longer chirp (0-5 Hz) was less than those of chirps of the call of F6 at a younger age and there was clear evidence of banding at *ca.* 1 and 4 Hz. To the human ear this call sounded similar to the previous vocalizations, except that it was of a lower pitch. In most respects, its features appeared to be intermediate between the "hiss-growl" of adult individuals and the distress hiss of pouch-young.

Features of the calls of F2 and F4 are shown in Figures 7.3.4 and 7.3.5. These were vocalizations of low frequency (0-5 Hz) and in records obtained for each animal banding was evident below 1 Hz and slightly above 4 Hz. The duration of each of the chirps was *ca.* 600 ms in each

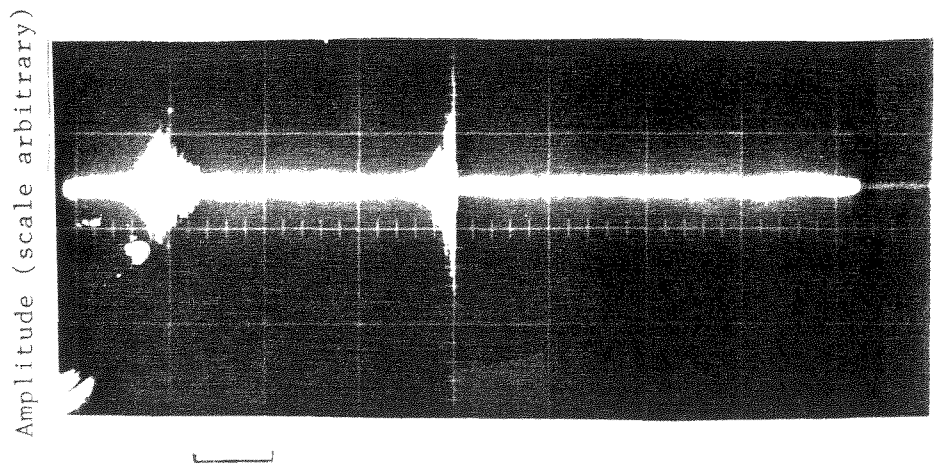
FIGURE 7.3.1: Oscillogram and sonogram of distress calls of F6 (166 days).

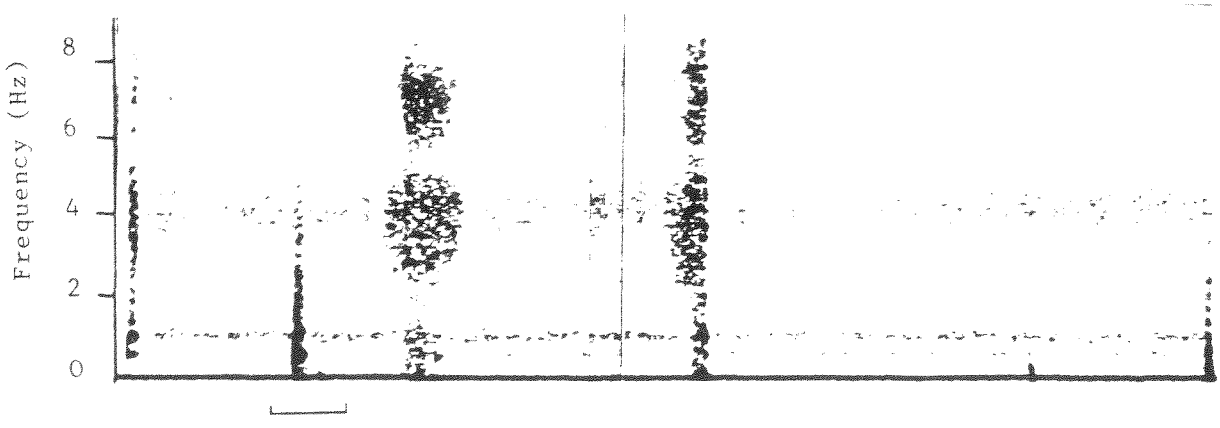
FIGURE 7.3.2: Oscillogram and sonogram of distress calls of M4 (155 days).





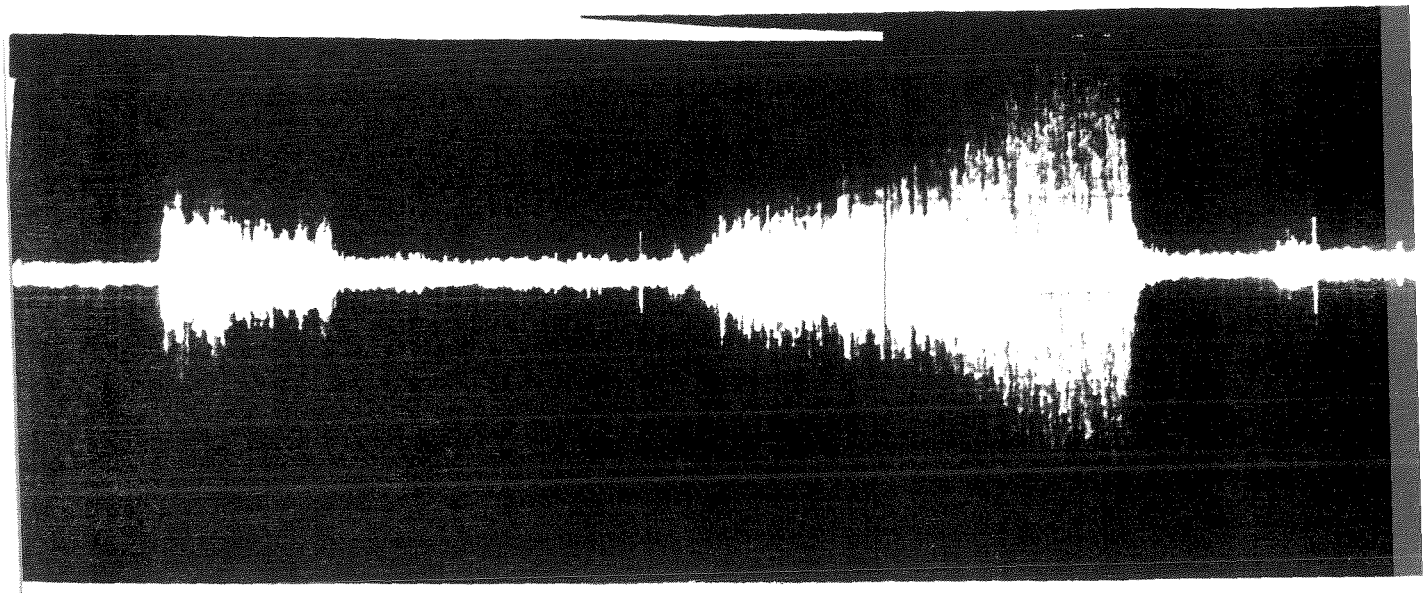
Scale 1cm : 200ms

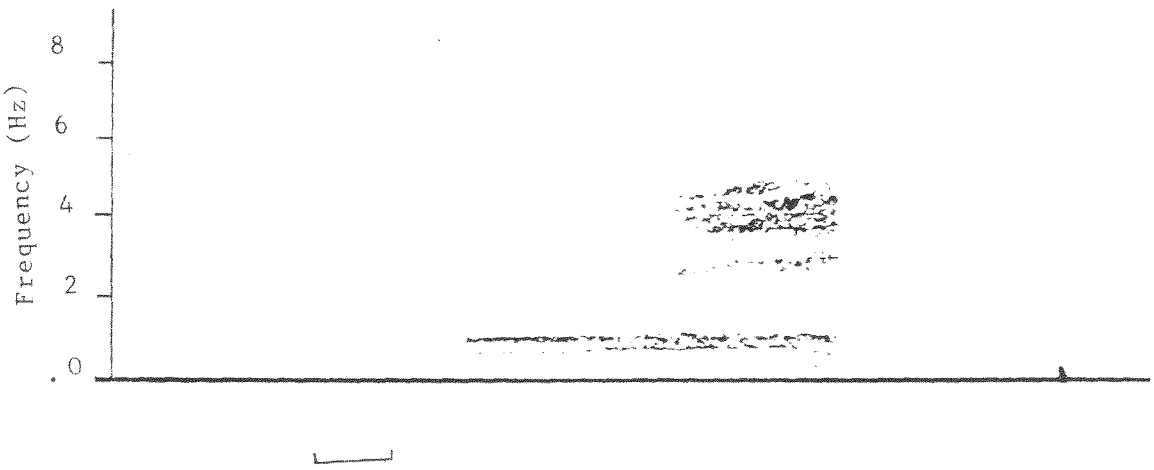




Scale 1cm : 200ms

FIGURE 7.3.3: Oscillogram and sonogram of calls of F6 (323 days). See text for discussion.

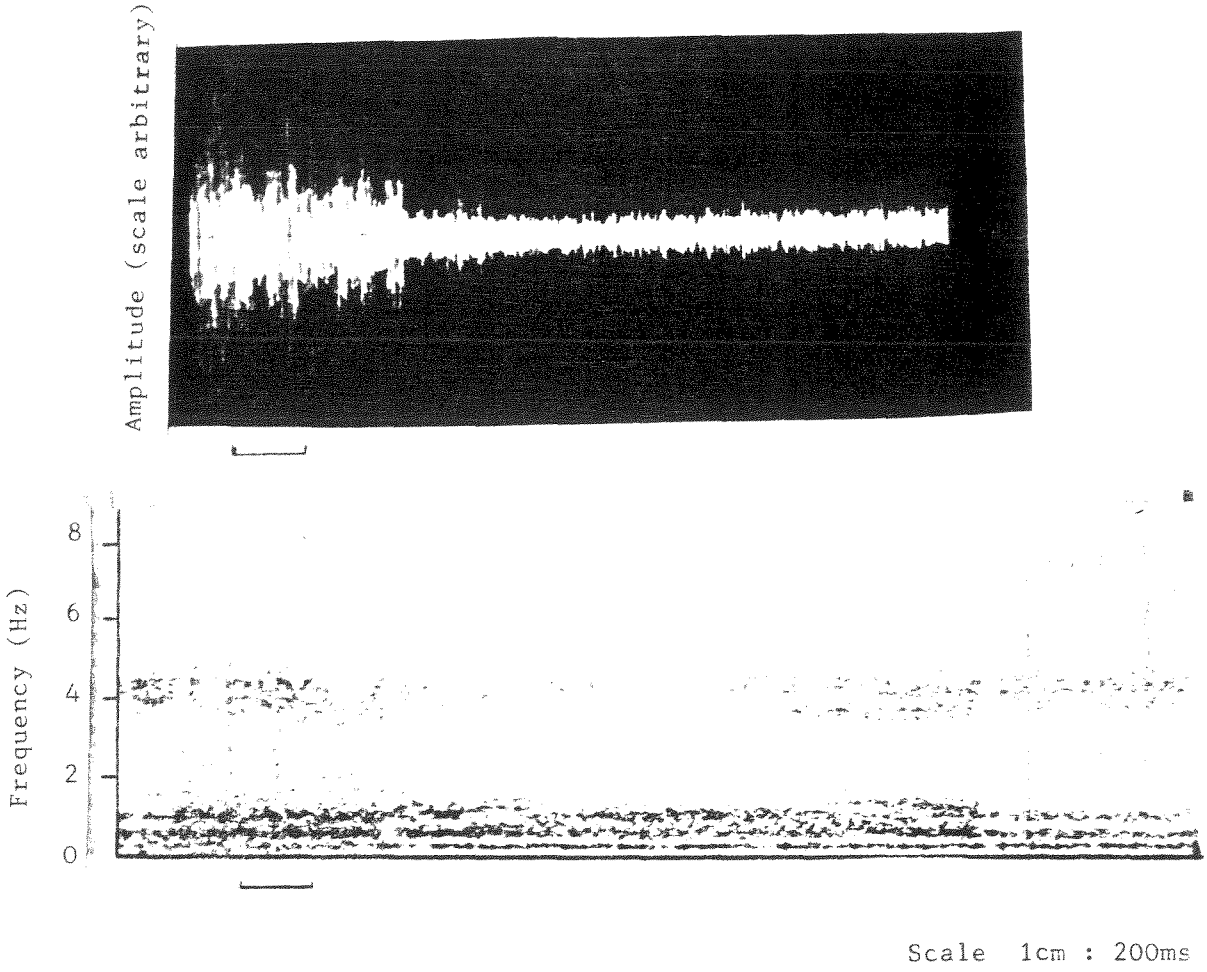




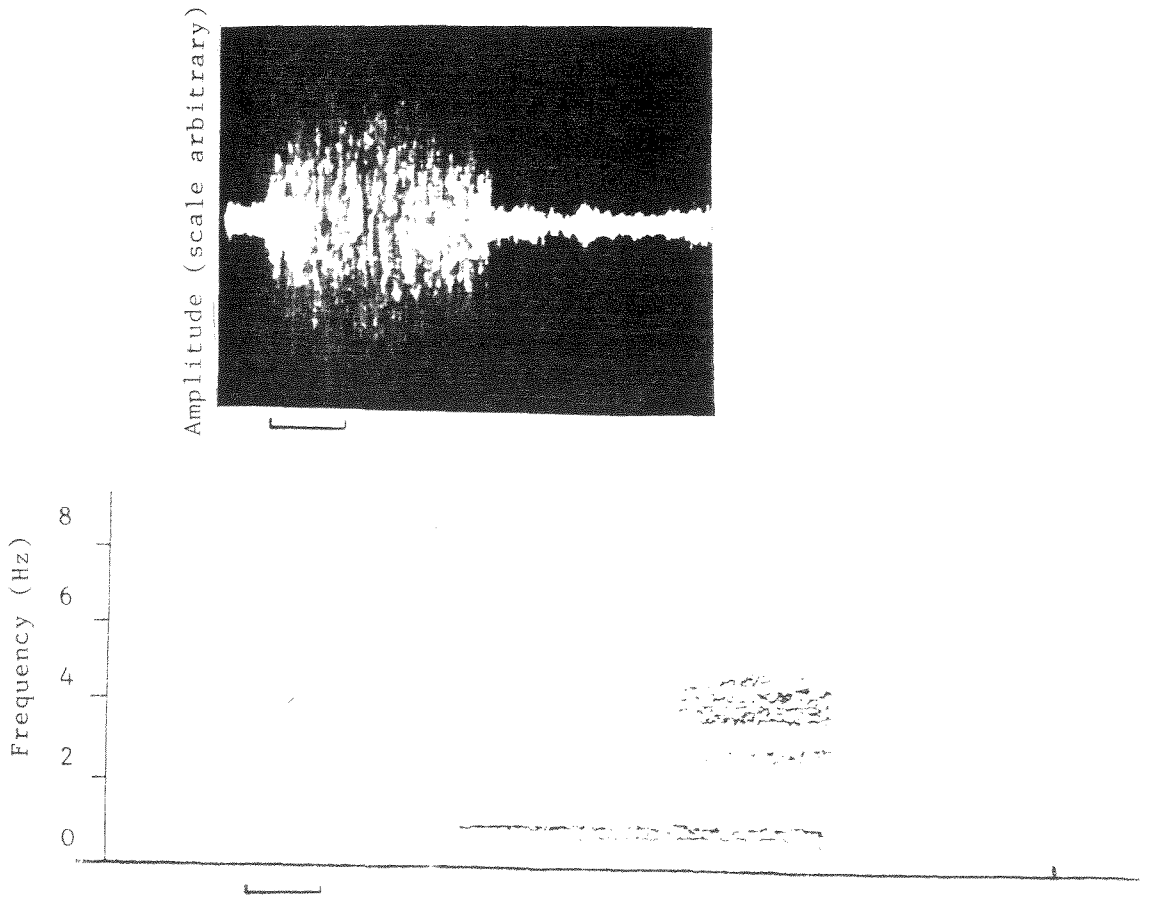
Scale 1cm : 200ms

FIGURE 7.3.4: Oscillogram and sonogram of call made by F2 when "harassed".

FIGURE 7.3.5: Oscillogram and sonogram of call made by F4 when "harassed".



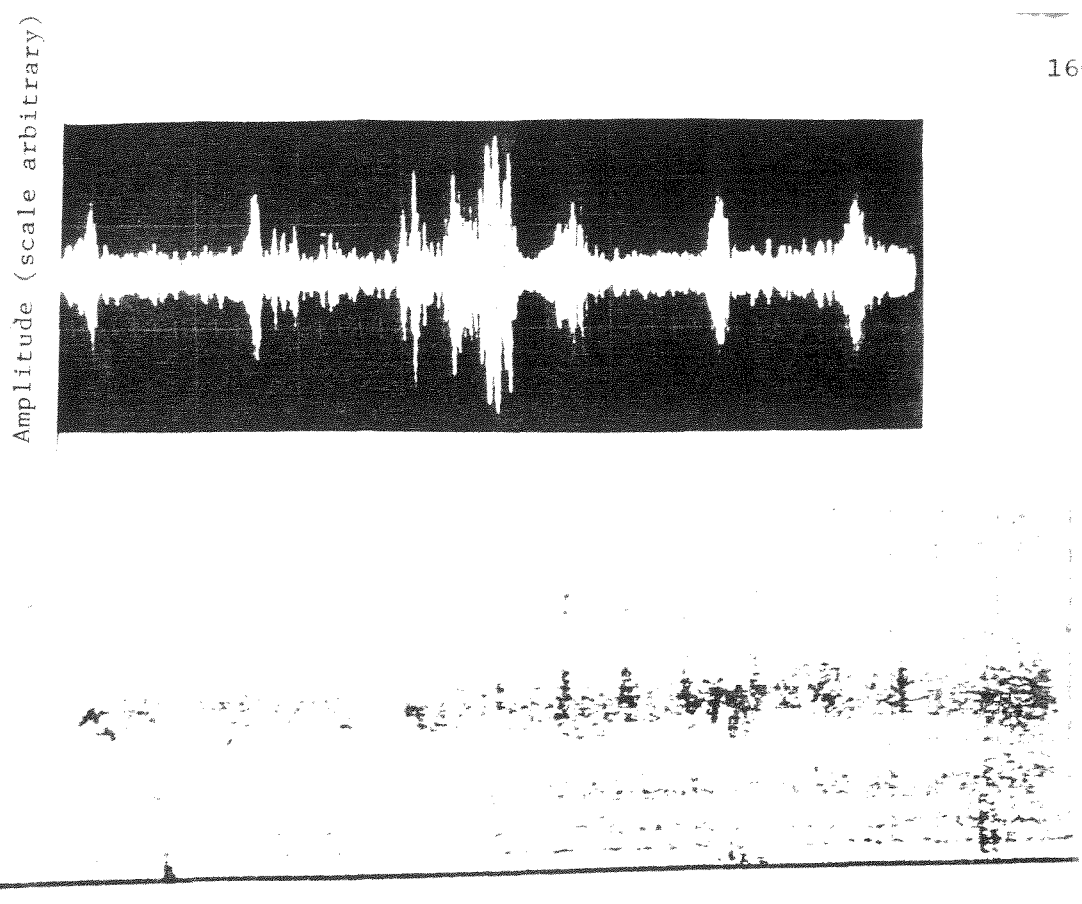
Scale 1cm : 200ms



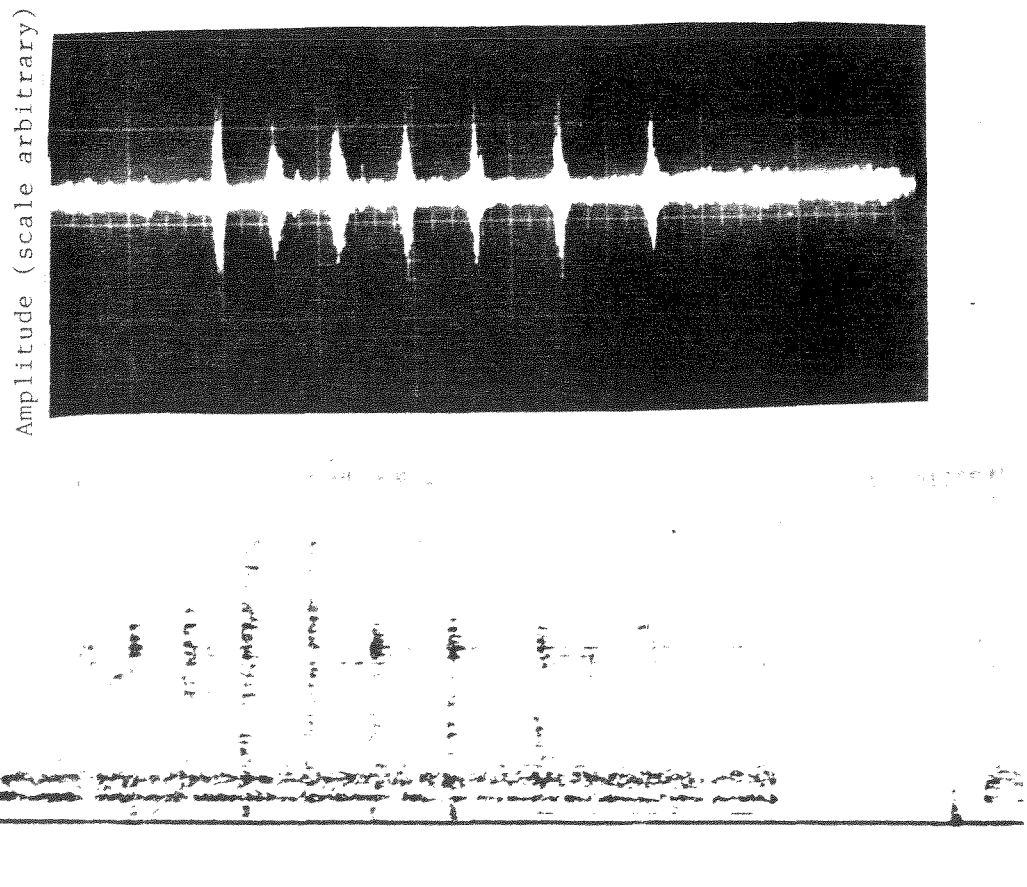
Scale 1cm : 200ms

FIGURE 7.3.6: Oscillogram and sonogram of calls made by M1 while associating with an oestrous female.

FIGURE 7.3.7: Oscillogram and sonogram of calls made by F1 when separated from it's pouch young.

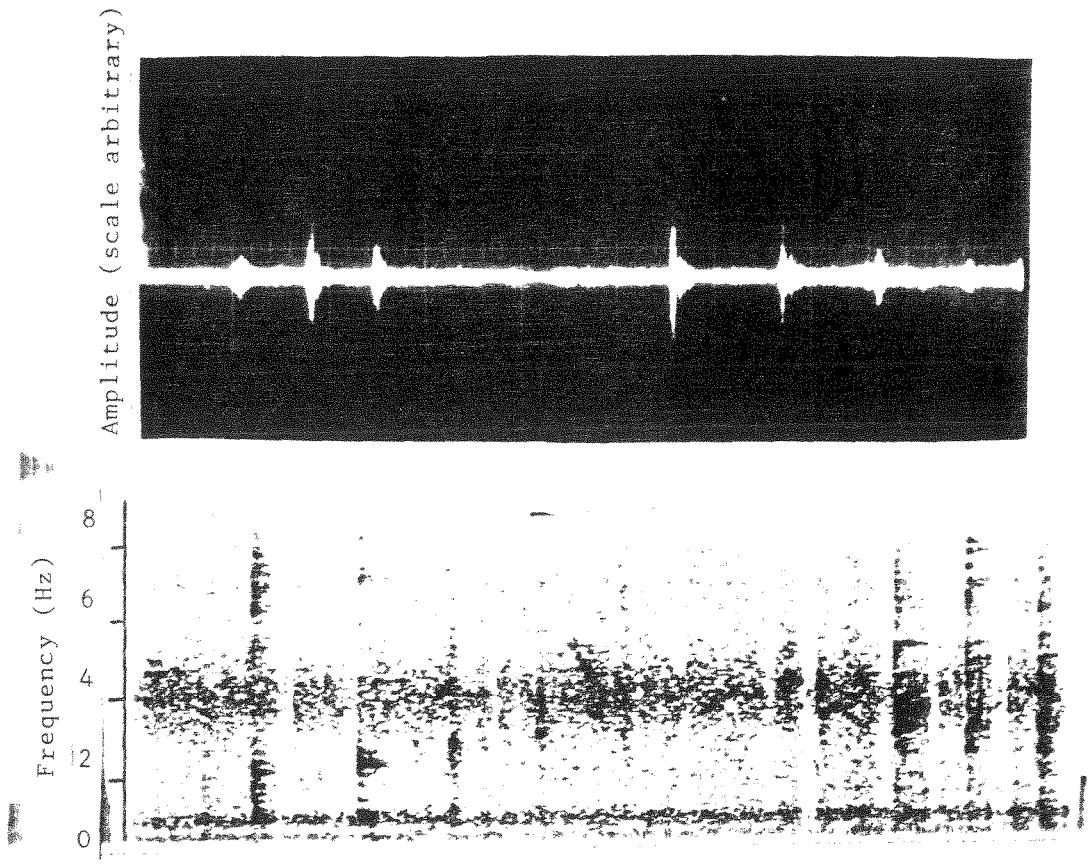


Scale 1cm : 200ms



Scale 1cm : 200ms

FIGURE 7.3.8: Oscillogram and sonogram of calls made by F5 when separated from it's pouch young.



Scale 1cm : 200ms

subject. These calls can be rendered onomatopoeically like a "hhrrrr" sound.

The sonograms and oscillograms produced from the calls of M1, F1, F5 are presented in Figures 7.3.6, 7.3.7 and 7.3.8. In each instance, the calls were characterised by chirps of short duration (*ca.* 50 ms) and the duration between individual chirps within each bout of calling was around 200 ms. The frequency-distribution for each chirp was relatively broad (0-8 Hz) in the calls of all three subjects; consistent banding also occurred at *ca.* 1, 4 Hz and possibly at 2.5 - 3 Hz.

7.4 DISCUSSION

7.4.1 The Structure of Vocalizations

Russell and Nicholls (1974) suggested that the function of distress calls of young *Macropus rufus* is to provide the mother with a means of locating it. This is presumably the function of distress vocalizations of young *Thylogale billardierii*. Marler and Hamilton (1966) stated that a wide range of frequencies in a call may provide cues for both intensity and phase difference, at the level of the two ears of the listener, whereas repeated sudden onsets and interruptions assist in the detection of binaural time differences. Therefore calls of this type may be useful in maximising the speed and accuracy of location.

The distress call of young *T. billardierii* exhibits these features. The two different types of chirps may also aid in locating the sources of calls.

The clucking vocalizations made by mothers also have a structure that is compatible with rapid localization of sources and is evidently even better suited for such a function than the sounds made by the young. All chirps are short, of large amplitude and have a large frequency-range. The structure of the call of the young is probably subject to greater restrictions, enforced by anatomical constraints, e.g. smaller lungs may

preclude the constant production of large amplitude chirps and the tongue may not be sufficiently well-developed to produce very sharp and discrete sounds.

No clear differences were apparent between the clucking of males and females. However, the quality of recordings of the vocalizations of M1 was generally poor and it is possible that sex-related differences do, in fact, exist. Males also emit such clucking vocalizations during agonistic interactions and these sounded identical to the author to clucking heard in the context of sexual following. Detailed analyses need to be performed in future in order to verify whether or not they are indeed identical. Since these vocalizations are always uttered while approaching another individual and in view of the structure of the clucking calls, they probably transmit to the recipient accurate information about the direction of the approach of the vocalizing conspecific.

The low-intensity growl (F2, F4), by contrast to the former types of vocalizations, are not structured so as to provide ease of location. It is of low frequency-range and long duration,with no abrupt onset or termination. Such properties may be expected to be associated with some defensive vocalizations, as in this context it is often desirable for the individual not to reveal its exact position.

It is possible that the hiss-grown vocalization of adult subjects develops by modification of the distress call of the young. These calls share some features although the hiss-growl is of a lower pitch and lacks the sharp cessation evident in most "hisses" of the young.

7.4.2 Comparison with the Vocalizations of Other Macropods

Distress vocalizations uttered by pouch-young and contact promoting vocalizations produced by the mothers have been reported in many species of Macropod. Female *Aepyprymnus rufescens* use soft grunts to call their pouch-young that have strayed from them and the young utter

similar vocalizations as they search for parents (Johnson 1980b). Squealing vocalization produced by young when searching for their mother and clucking vocalizations made by the latter seeking to re-establish contact with their young have been reported in *T. thetis* (Johnson 1977a), *M. parryi* (Kaufmann 1974) and in *M. rufus* (Frith and Calaby 1969; Russell 1970b; Croft 1981a). Young *M. robustus erubescens* emit repeated clucking vocalizations when alarmed which attract the attention of their mothers (Croft 1982). The distress call of young *M. parryi* becomes more similar to the loud clucking of adult females as they mature (Kaufmann 1974a) and this may also be the case in *M. rufus* (Russell 1970b).

Clucking by males engaging in sexual following of female have been reported in *M. rufus* (Frith and Calaby 1969; Russell 1970b; Croft 1981a), *M. parryi* (Kaufmann 1974a), *M. giganteus* (Grant 1974), *M. rufogriseus* and *Wallabia bicolor* (Sharman *et al.* 1966), *T. thetis* (Johnson 1977a) and *Bettongia lesueuri* (Stodart 1966). Differences between clucking in males and in females are believed to exist in some species (Russell 1970a; Kaufmann 1974a; Johnson 1977a), usually distinguished as "soft" clucking in the former and "loud" clucking in latter. Clucking by males in the context of agonistic interactions has been noted in *M. rufus* (Frith and Calaby 1969).

Vocalizations during agonistic interactions are of common occurrence in members of the family Macropodidae. Male and female *T.thetis* uttered a call similar to that produced by *T. billardierii* (Section 7.3) when subjects were handled by the investigator and during aggressive encounters (Johnson 1977a). Kaufmann (1974a) described a "hiss-growl" used by females as being characteristic of defensive threat. This call was uttered by females when they were approached by males and was also often made by females attacking or being attacked by other females. *M. robustus erubescens* produce a guttural hiss when threatening another individual, i.e. when approaching another animal in the high standing position and fleeing individuals commonly give a repeated "hiccoughing"

call (Croft 1981b).

A "cough" vocalization is also emitted during agonistic interactions in *M. parryi, M. fuliginosus, M. giganteus* and *M. antilopinus* (Croft 1982). In *M. parryi* this vocalization is primarily a sign of fear or submission (Kaufmann 1974a). *M. rufus* utter a "Ha" vocalization in agonistic interactions (Russell 1970b, Croft 1981a).

Female *T. brunii* produce an aggressive coughing sound (*hustende und keckernde Laute*) during fights (Ganslosser 1978). Subordinate female *Aepyprymnus rufescens* growl when they are attacked by conspecifics and a similar vocalization is made by females while they are sexually investigated by a male (Johnson 1980b). *B. lesueuri* squeal when they are under attack and while warding off unrequited advances by males (Stodart 1966).

Members of some species emit alarm calls when they are disturbed (for example, by the approach of human intruders). Such vocalizations are usually accompanied by the "alarm foot thump". *M. antilopinus* and *M. robustus erubescens* and *A. rufescens* utter a loud hiss in the same context (Croft 1982, Johnson 1980b). *B. lesueuri* also grunt when they are disturbed.

Although it is difficult to draw definite conclusions about vocal communication in macropods, there is, apparently, a generally consistent schema of affinities and *T. billardierii* appears to conform in this respect.

CHAPTER 8

GENERAL DISCUSSION AND CONCLUSIONS

The results of the study of diel activity-patterns indicate that representations of activity-cycles based on only a limited number of criteria or on indirect (i.e. non-observational) methods of data-collection may yield misleading results. For example, captive *Thylogale billardierii* exhibit a relatively constant diel level in the performance of comfort behaviours, but resting behaviour is generally confined to a few periods of the day and even while resting, the subjects were not necessarily inactive in terms of being asleep. Harcourt (1978) suggested that patterns of social interaction, (i.e. the types, structure and participants of social interactions) not only their frequencies may change through the day. This concept may also be expanded to include all types of activities e.g. sequences of grooming, escape responses to predators, modes of resting and any such changes are presumably important in the biology of the species under scrutiny.

The fact that the majority of species of macropods tend to be most active nocturnally has often been noted (e.g. Russell 1974a,b; Kaufmann 1974a; Coulson 1978); however, behavioural studies on macropodines have, in general, ignored nocturnal behaviour, particularly in the case of the larger species. During this course of the study, ritualized fights between males were observed in the daytime on only a very few occasions. The "resting together" behaviour was also more prominent at night; both in male-females and in mother-offspring dyads. In the author's opinion, these observations emphasize the necessity of examining complete diel cycles of behaviour.

It must be reiterated that patterns of behaviour exhibited by captive individuals may be at variance with those exhibited by their free-living conspecifics and extensive field-studies are required on *T. billardierii* in order to verify the results of this study, in this

respect.

Investigations of the possibility of differences in feeding and/or digestive strategies between individuals of different sex and reproductive status (especially in relation to the effects of pouch-young) appears to be an area of research that may yield interesting results. Since the greater proportion of this study has been completed an investigation of the morphology of the digestive system of *T. billardierii* has been brought to the attention of the author indicating that this species differs markedly from the other members of the genus thus far investigated (Dellow 1979 after Hume 1982).

T. billardierii is exposed to much colder climates than most other species of macropods and this may involve certain behavioural requisites of adaptations; however, this has not been investigated to date. It is suggested that the "resting-together" behaviour of mother and young may be advantageous in conserving the body-heat of the young, possibly alleviating some of the problems caused by the sudden changes in environments at the termination of pouch life. Frith and Calaby (1969) found that mortality in the pouch-young of *M. rufus* was greatest at the time when the young were on the point of vacating the pouch permanently. In this species, drought is a major influence in increasing mortality of pouch-young. It is possible that cold may represent some hazards to young *T. billardierii* vacating the pouch.

The existence of consistent and well-defined social relationships, observed in the captive group in this study needs to be related to and investigated more fully in field studies. Johnson (1978) found that male *T. billardierii* have common home-ranges; however, whether or not this is also the case in females, is not known. From the present study, it is apparent that social hierarchies may exist between female individuals and these are relatively stable and their maintenance need not depend on constant reinforcement by agonistic interactions.

There is strong evidence for the importance of olfactory communication in individual recognition, agonistic interactions and sexual interactions, therefore the possible presence of semiotically functional glands in this species should be investigated in the future.

The function of the various behavioural events identified in sexual interactions are yet to be fully explained. It is undoubtedly the intention of males to attempt to ascertain the reproductive states of females but how precisely tuned are the cues by which they obtain such information from the latter, are not known in this species or any other macropod. Detailed analyses of changes in the behaviour of males as females approach oestrous also need to be undertaken in relation to such phenomena.

The occurrence of visual displays in the course of agonistic interactions is apparently paradoxical in view of the nocturnal habits of *T. billardierii*. The grass-pulling display, although it was distinctive and conspicuous had no obvious effects on other individuals; however, more detailed studies of the sequences of events involved in such activities are required.

In conclusion, the behaviour of *T. billardierii* is apparently similar in many respects to those of the larger macropods; however, this species differs in its social organization from the majority of the species so far investigated.

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APPENDIX 1

DETAILS OF SUBJECT USED DURING THE COURSE OF THE STUDY

APPENDIX 1 Details of *Thylogale billardierii* subjects used during the course of this study (M = male, F = female).

Subject	Date	Weight	Comments
M1	24/3/82	6.7 kg	In lower enclosure
	12/8/82	10.1 kg	"
	2/10/82		Dead v. Appendix 2
M2	7/3/82	6.8 kg	In upper enclosure
	2/8/82	7.0 kg	Placed in lower enclosure
	4/10/82	7.3 kg	
M3	24/3/82	4.1 kg	In lower enclosure
	26/4/82	4.3 kg	Age 50-60 weeks, Testicular Index 13.2*. No sperm present in urine
	12/8/82	5.5 kg	Urine with sperm
	7/10/82	6.2 kg	Removed from lower enclosure
M4	3/5/82	-	Pouch young of F5, to young to remove from teat
	12/8/82	180 g	Head 5.7 cm, pes 6.2 cm, tail 10.3 cm* Age = 138 days†
	1/9/82	346 g	Head 6.3 cm, pes 8.0 cm, Age = 155 days
	9/9/82	263 g	Head 6.75 cm, pes 8.0 cm, tail 13.35 cm Age = 168 days Dead
M5	1/6/82	-	Pouch young of F1, 1 day old
	7/10/82	181 g	Head 5.35 cm, pes 6.2 cm, tail 10.0 cm Age = 128 days
F1	17/3/82	6.75 kg	With pouch young (F6). In lower enclosure
	1/6/82	5.67 kg	With pouch young (M5)
	7/10/82	6.1 kg	"
F2	4/8/82	6.5 kg	In upper enclosure. No pouch young
	30/8/82	6.1 kg	With pouch young. Placed in lower enclosure
	4/10/82	6.1 kg	No pouch young
F3	24/3/82	5.3 kg	In lower enclosure. No pouch young
	7/10/82	6.3 kg	With pouch young (F7). Removed from lower enclosure

APPENDIX 1 (continued)

Subject	Date	Weight	Comments
F4	24/3/82	4.4 kg	In lower enclosure. No pouch young
	20/9/82		No pouch young
	7/10/82	5.6 kg	"
F5	18/3/82	4.15 kg	In lower enclosure. No pouch young
	3/5/82	4.6 kg	With pouch young (M4)
	12/8/82	5.24 kg	"
	1/9/82	5.4 kg	"
	28/9/82	5.2 kg	With very small pouch young *ca.* 2 days old
F6	17/3/82	135 g	Pouch young of F1 Head 4.9 cm, pes 5.0 cm, tail 9.0 cm Age = 115 days
	26/4/82	409 g	Head 6.3 cm, pes 8.4 cm, tail 9.0 cm Age = 155 days
	5/5/82	507 g	Age = *ca.* 166 days
	31/5/82	810 g	Head 6.9 cm, pes 9.4 cm, tail 22 cm Age = 172 days
	26/8/82	1.8 kg	Age = *ca.* 273 days. Permanently out of pouch at this stage
	20/9/82	2.5 kg	
F7	7/10/82	-	Pouch young of F3 Head 4.7 cm, Age = 109.2 days

* Measurements of all parameters based on the methods of McCartney (1978).

† Ageing of pouch young based on formula of Rose and McCartney (1982b).

APPENDIX 2

RESULTS OF AUTOPSY PERFORMED ON CARCASE OF M1

APPENDIX 2 Results of autopsy performed on the carcase of M1, 6/10/1982 (B. Munday *pers. comm.*).

A.2.1 Macroscopic Lesions

General condition - very fat. Liver showed zonal necrosis.

Pale streaks present under the endocardium (possibly fat tissue).

Anoplotaenia dasyuri (Cestoda) present in the myocardium.

Dipetalomena thylogali (Cestoda) present in the peritoneal cavity.

Localized area of thickening and reddening of stomach mucosa.

A.2.2 Histopathology

Brain - mild perivascular cuffing.

Heart - mild myocarditus.

Lung - congestion and oedema.

Liver - periacinar necrosis, some hepatocytes showed margination of the nuclear chromatin and condensation of the nucleous (possibly inclusion bodies present).

A.2.3 Diagnosis

A definite diagnosis was not possible, but infection of the animal by a herpes virus was a possibility.

APPENDIX 3

NOTES ON THE EFFECTS OF BROMOCRIPTINE ON LACTATING FEMALES

APPENDIX 3 Notes on the effect of bromocriptine (CB154) on lactating female *Thylogale billardierii* (based on data obtained by Mr. R. Rose).

A.3.1 Introduction

Bromocriptine has been found to have an inhibitory effect on prolactin secretion in various experimental animals (resulting in an inhibition of lactation) by interacting directly on the prolactin (secretory) cells (Flückiger 1980). The administration of bromocriptine to lactating female *Macropus eugenii* has been shown to induce reactivation of diapausing blastocysts except during period of seasonal quiescence from September to December (Tyndale-Biscoe 1979).

Mr. R. Rose of the University of Tasmania, has been running an extended project on the effect of the administration of bromocriptine on lactating *Thylogale billardierii*.

A.3.2 Methods

Bromocriptine was administered at a dosage rate of 5 mg per kilo of body weight, to lactating female *Thylogale billardierii*. Dates of administration are shown in the results. During this study three females were injected with the drug.

A.3.3 Results

The results of the observed effects of bromocriptine in experimental subjects are summarised in Table A.3.1.

From these results it seems likely that the pouch life of F6 was terminated early.

TABLE A.3.1 The effects of bromocriptine on lactating female *Thylogale billardierii*.

Date of Administration	Subject	Weight of pouch young	Comments
5/5/1982	F1	307 g	Birth 25 days later and oestrous (probably). Old pouch young (F6) out of pouch permanently. Age 188 days weight 810 g.
5/5/1982	F5	?	Very small pouch young, (M4), *ca.* 3 weeks old at time of injection. No positive responses.
1/9/1982	F5	346 g	Birth 25 days later and oestrous (Mating). Old pouch young died 9/9/1982.
1/9/1982	F2	?	Small pouch young. No obvious effects, pouch young lost at some stage (by 4/10/1982). Mated 5/11/1982.

APPENDIX 4

GROUP SIZES IN THE MACROPODIDAE

APPENDIX 4

GROUP SIZES IN THE MACROPODIDAE

A.4.1 INTRODUCTION

Estimations of group sizes in a given species may provide useful information about its social organization. Jarman (1974) attempted to relate the sizes of groups of individuals of several species of Bovidae to various factors pertaining to their ecology and behaviour. Similarly to much of the relevant general literature, data on group sizes in macropodids is fragmented by comparison with that relating to eutherians. Sizes of groups have been measured in red kangaroos (*Macropus rufus*) by Caughley (1964), Frith (1964), Russell (1979) and Croft (1981a), and in eastern grey kangaroo (*M. giganteus*) by Caughley (1964), Kirkpatrick (1966), Kaufmann, (1974b,c, 1975) and Taylor (1982). Also in the whiptail wallaby (*M. parryi*) by Kaufmann (1974a,b,c), in the euro (*M. robustus*) Kaufmann (1974a,b,c), Croft (1981b) and Taylor (1982), the red-necked wallaby (*M. rufogriseus*) and the swamp wallaby (*Wallabia bicolor*) by Kaufmann (1974a,b,c) and in the agile wallaby (*M. agilis*) by Johnson (1980). Apart from these studies, no quantitative studies of group sizes are available in macropods.

Since 1977 the National Parks and Wildlife Service of Tasmania has been conducting surveys of Forester kangaroos (*M. giganteus tasmaniensis*) in two localities of the Tasmanian Midlands. The present author was permitted to examine data collected during the period 1977-1979, also participated in one survey during the current year (1982), thereby providing an opportunity to gain experience with the methods used for obtaining such information. The surveys generated data from which it was possible to estimate group sizes of both *M. giganteus tasmaniensis* and Bennett's wallabies (*M. rufogriseus frutica*).

A.4.2 METHODS

Surveys were conducted by employees of the National Parks and Wildlife Service in the Ross and Nile districts, at various times during each year from 1977-79. The actual months in which data were obtained are indicated in the tabulation of the results. In both of the areas sampled the habitat comprised eucalyptus woodland and open forest situated on undulating country adjacent to natural grasslands, marshes and paddocks of improved pasture. Rainfall averages 550 mm per annum and the highest values are recorded in the winter, the lowest in the summer, at least 33 mm falls each month. Ranges of mean maximum and minimum temperatures are: February, 24.2 - 9.3°C; June, 11.3 - 0.5°C (Pearse 1981).

Along each of the transects examined, all identified species of mammals were noted, their numbers, distances from observer, the angle of their positions to the transect line (to the nearest 45°), habitat type (grassland/pasture, woodland, forest, scrub) and the broad categories of their ongoing behaviour (lying, standing, feeding, moving). The sex and age (adult or juvenile) of individuals were noted wherever possible. Forester kangaroos, Bennett's wallabies and fallow deer (*Dama dama*) were frequently encountered; other species of mammals were sighted only on rare occasions; these included pademelons (*Thylogale billardierri*), rabbits (*Oryctolagus cuniculus*) and echidnas (*Tachyglossus aculeatus*).

A.4.3 RESULTS

(a) Forester Kangaroo

The data shown in Table A.4.1 is for a total of 1720 kangaroos from surveys in September 1977, January 1978 and May 1978 in the Nile region and 935 kangaroos in the Ross area in May 1978. Group sizes

TABLE A.4.1 Analysis of Group Size for Forester Kangaroos and Bennett's Wallabies.

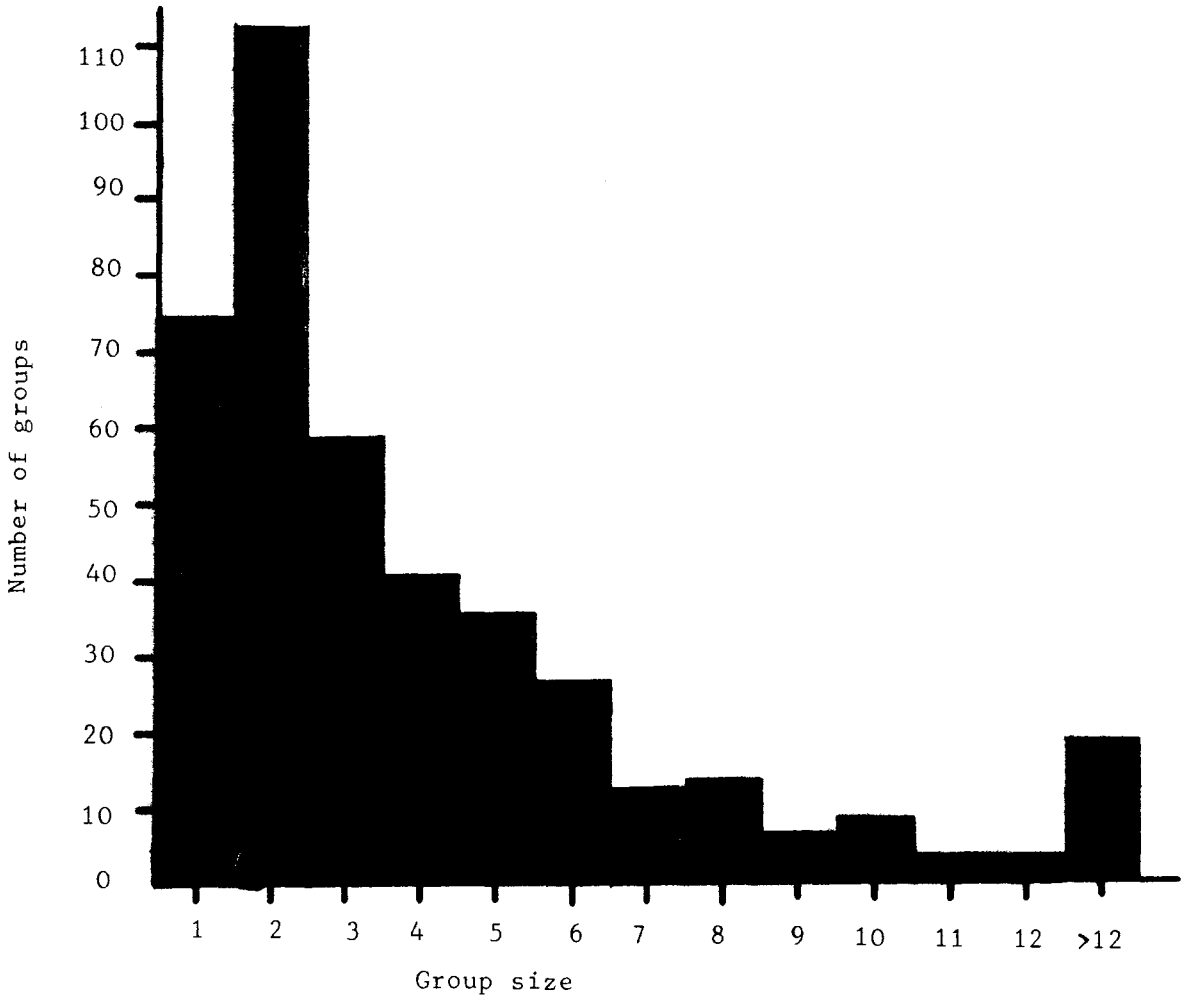
Species	Site	Mean Group Size	Typical Group Size	Percentage Single	Number of Groups
M. giganteus tasmaniensis	Nile	3.60	5.39	5.31	1412
	Ross	3.82	6.04	4.70	935
M. rufogriseus frutica	Nile	1.64	2.50	39.9	599

exceeding twelve individuals were excluded from consideration in all estimations. Due to the method of data-collection employed there was a tendency for animals to move along ahead of the observer and joining other groups, thereby forming larger mobs. However, since such unrealistically large groups were rare, their omission from analysed data probably did not greatly affect the estimated means. Groups of up to 20 individuals were seen feeding, standing or resting undisturbed, so it is postulated that estimates of group sizes will be conservative.

Typical group sizes were calculated similarly to the methods used by Jarman (1974) and express the mean size of the group in which individuals of the species most commonly occur. The distribution of frequencies of group sizes of the two sampled populations are shown in Figure A.4.1. An illustration of group sizes related to their cumulative frequencies on a scale of normal probabilities is given in Figure A.4.2. The compositions of 340 groups from the Nile region (April 1977, June 1977, September 1977, January 1978, May 1978, May 1979) and of 223 groups in the Ross area (May 1977, May 1978, July 1979) are shown in Table A.4.2. Only groups in which every individual was sexed and aged were included. There is a general inaccuracy against large groups, larger groups usually being sighted from greater distances and generally while they are moving, rendering them very difficult to sex.

FIGURE A.4.1 The frequency distribution of group sizes of two populations of Forester kangaroos.

(a) Nile



(b) Ross

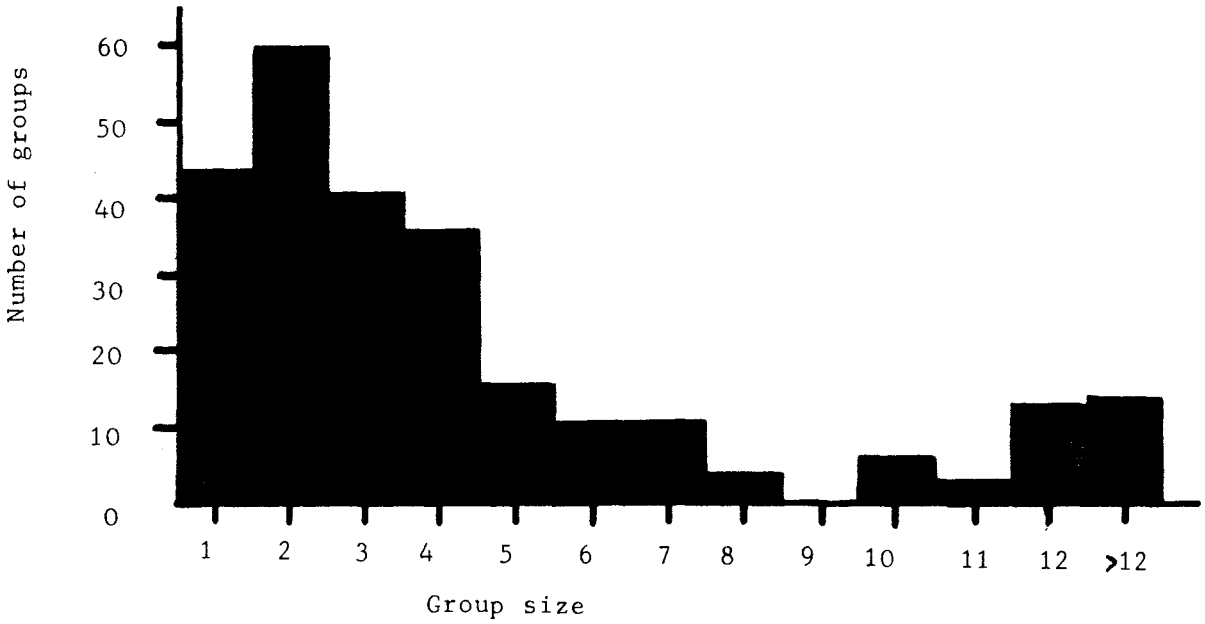


FIGURE A.4.2 Numbers per group of Forester kangaroo and Bennett's wallaby plotted against their cumulative frequencies on a normal probability scale.

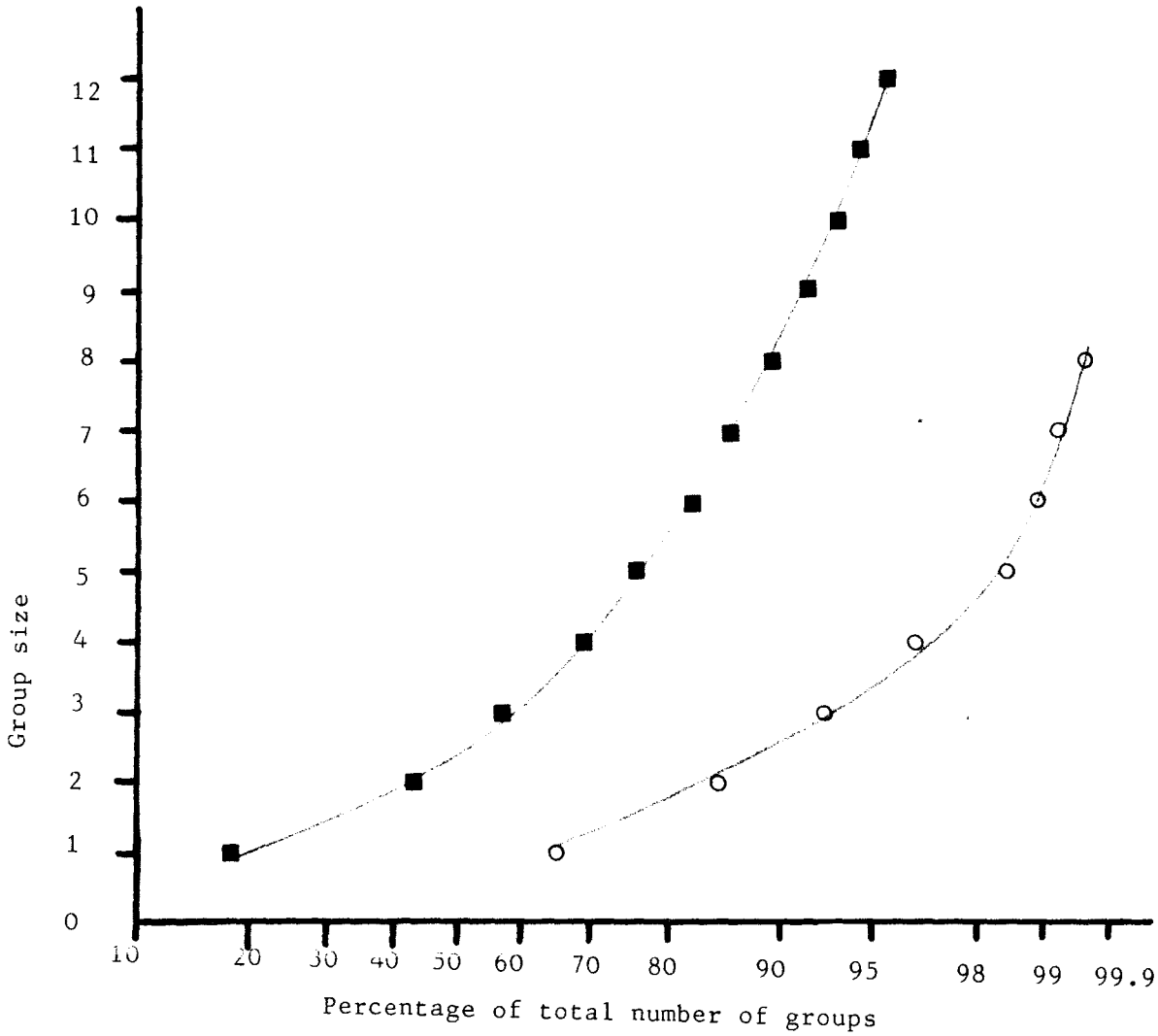


TABLE A.4.2 Composition of 563 Groups of Forester Kangaroos. M - male; F - female; J - juvenile.

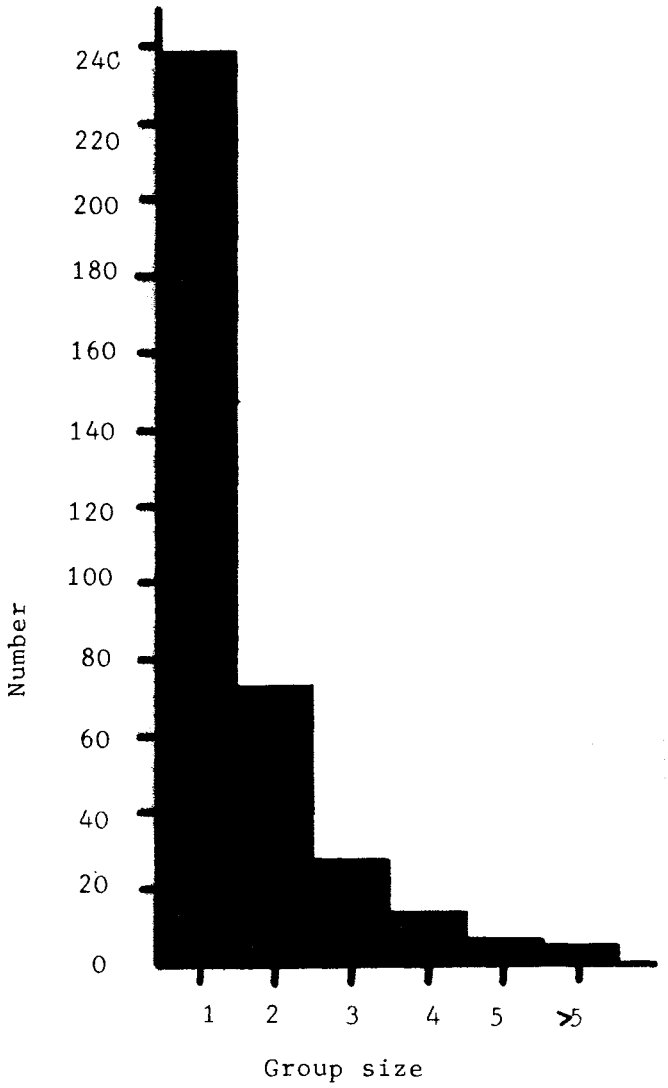
Group Composition	Percentage of Groups	
	Nile	Ross
M	21.2	22.9
F	3.8	2.2
J	2.1	1.8
MF	4.4	10.8
FJ	28.8	12.1
MFJ	11.5	10.8
OTHER	28.2	39.4

Nevertheless, groups ranging in size to a maximum of forty-eight were sexed. Thirty two percent of all males were observed to occur singly, whereas only 4% of females and 25% of juveniles were alone. Twelve percent of males were found in groups of two, 39% of females and 38% of juveniles (these data are based on the Nile population only).

(b) Bennett's Wallaby

Data shown in Table A.4.1 are based on 599 individuals surveyed at Nile in April 1977, June 1977 and September 1977. The frequency distribution of these is shown in Figure A.4.3. These wallabies were most frequently flushed out of resting places in gullies, usually situated amongst dense scrub; the disturbance of one individual resulted in a type of chain-reaction and this resulted in great difficulties when attempting to resolve whether animals were sojourning together or not. In general, it can be stated that Bennett's wallabies are essentially solitary animals. Group sizes related to cumulative frequencies on a scale of normal probability are shown in Figure A.4.2.

FIGURE A.4.3 The frequency distribution of group sizes of Bennett's wallabies.



Very limited amounts of data were available on the sex and ages of these wallabies, consequently the compositions of groups could not be accurately determined.

A.4.4 DISCUSSION

Group sizes obtained for various species of the subfamily Macropodinae are shown in Table A.4.3. It is evident from this that Tas-

TABLE A.4.3 Comparison of group sizes in macropods.

Species	Number of Groups	Percentage Single	Mean Group Size	Typical Group Size	Source
Macropus giganteus	174	12	3.3		Caughley 1964
	272	34			Kirkpatrick 1966
			3.9		Bell 1972*
			2.1		Taylor 1975*
	136	22	3.7		Kaufmann 1975
	53	4	6.4		" "
			2.5		Southwell 1976*
	564	16.3	4.49	8.81	Taylor 1982
	162	22.2	2.96	4.36	" "
M. fuliginosus			2.5		Coulson (after Croft 1982)
M. rufa	106	25	2.5		Caughley 1964
	193	6			Frith 1964
	760	18	2.6	3.7	Russell 1979
	613	*ca*.23	2.2	3.7	Croft 1981a
M. parryi	2185	*ca*.18.5	6.0		Kaufmann 1974a, b,c
M. robustus			1.4		Russell & Richardson 1971
	153	*ca*.46	2.1		Kaufamnn 1974b,c
	366	40	2.1	2.6	Croft 1981b
	1610	43.2	2.17	3.55	Taylor 1982
	233	54.5	1.79	2.60	" "
M. agilis	583	68	c1.7		Johnson 1980
M. rufogriseus banksianus	739	*ca*.68	1.5		Kaufamnn 1974b,c
Wallabia bicolor	58	*ca*.88	1.1		Kaufmann 1974b,c
M. antilopinus			2.5		Russell & Richardson 1971
	356	3	4.5		Croft 1982
M. parma	71	73.2	1.34	1.61†	Maynes 1977

* After Taylor 1982

† Calculated from Maynes Data

manian subspecies of *M. giganteus* has a similar mean group size to the mainland subspecies. Grant (1973) found a very high frequency of single kangaroos but this is probably due to his highly restrictive definition of a 'group' (Kaufmann 1975). Whether these groups of *M. giganteus tasmaniensis* are stable or continuously changing was impossible to establish; however, Kaufmann (1979) in a study of *M. giganteus* at Gorge Creek, near Bonalbo, New South Wales, suggested that the groups are relatively stable and consist of varying combinations of individuals from discrete mobs. He based these notions on the feasibility of repeated recognition of some individuals.

Caughley (1964) presented a statistical argument for a random process of group formation, since no groups (except 'groups' of size one) deviate from normality, suggesting that animals join and leave randomly. A similar approach is used in treating the data obtained from the Nile region (September 1977, January 1978, May 1978). Normality is only exhibited by group sizes of seven and above. Similarly to Caughley's population, there was a sharp truncation at the level of 'groups' of one animal but groups of two to six also deviate (by gradually diminishing degrees) from the straight-line expectation, indicating the existence of a skewed distribution.

This deviation may be explained examining the sex/age composition of the groups. The most frequently occurring groups were female-juvenile pairs and lone males; there was also a high percentage of male-female-juvenile trios (Table A.4.2). Caughley (1964) commented on the apparently close association (lasting for some time after weaning) of juveniles with their mothers. Kirkpatrick (1966) states that the family group of a female and her most recent young was the basic unit of organization rather than the individual (after Kaufmann 1975).

The large number of male-female and male-female-juvenile associations is difficult to explain, given that these animals are seasonal breeders, with a marked summer peak of reproductive output (Pearse 1981;

Poole and Pilton 1964); however, they are also known to breed at all periods of the year.

A detailed study of marked or otherwise recognizable individuals is necessary in order to examine the nature of associative relationships within a species of macropod. Having a mean group size of ca. three-four, *M. giganteus* is intermediate in sociability between *M. parryi* (Kaufmann 1974a,b,c) and *M. rufa* (Caughley 1964; Russell 1979; Croft 1981). The large typical group size of *M. giganteus tasmaniensis* (Table A.4.1) also reflects the degree of positive association between individual animals. Whether or not the animals interact to any substantial extent within groups, does not effect the probability that groups will be of a general size yielding the greatest adaptive value.

Kaufmann (1974c) suggests the existence of a number of behavioural adaptations that facilitate group-formation in *M. parryi* viz. grazing habits (which permit the attainment of relatively dense populations and sustain large aggregations in restricted areas). They are of moderate body size which, coupled with their grazing habits, leads to a preference for an open habitat, and their mobility and partly diurnal habits facilitate group-coordination. These considerations are probably also applicable to *M. giganteus;* however, the latter are less diurnal than *M. parryi* (Caughley 1964). Kaufmann (1974c) believes that predation-pressure is the major factor leading to increased sociality in the larger, more mobile species of macropods.

M. rufogriseus frutica appear to be typical of the medium-sized macropods, having a mean group size of ca. 1.6. *M. rufogriseus* (Kaufmann 1974b,c), *M. agilis* (Johnson 1980), *W. bicolor* (Floyd 1980; Kaufmann 1974b,c) are all essentially solitary. This is to be expected, in view of their general habits. All of them frequent dense scrub when resting and move out to pastures and grasslands to feed, generally at night. These wallabies also appear to be less mobile than the larger macropods having smaller home ranges, although few studies have been

done to define home ranges accurately except in *W. bicolor* (Edwards and Ealey 1975).

Data on sex and age were not available for *M. rufogriseus frutica* but the majority of groups of two consisted of mother-juvenile pairs (R. Pearse pers. com.).

Browsing habits, contrasting with grazing, has been suggested as a potential factor in determining group-sizes in Bovidae (Jarman 1974) and although the correlations between these are not as well-defined as in Macropodidae (Kaufmann 1974c), their possible influence cannot be disregarded.

One aspect that should be stressed is that these estimates of group-sizes were obtained from data collected during the day, although the animals are apparently mainly nocturnal; hence estimates obtained may be too conservative.

In conclusion, the need for further investigation in this area of the ecology and behaviour of macropods must be emphasised. Group-composition and individual relationships are virtually unknown in most species of the Macropodidae and even in those species of the family that have been studied these aspects are poorly understood. Such information is essential to understanding the evolution of the family and for devising techniques of management and conservation.